THE UNIVERSITY OF ALBERTA

# ALLOCATION AND DYNAMICS OF CARBON IN TWO SOILS CROPPED TO BARLEY

BY

GORDON DAVID DINWOODIE

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## Abstract

Allocation and microbial use of $^{12}C$ and the distribution and dynamics of $^{14}C$ after pulse labelling with $^{14}CO_2$ were studied in barley plots on a Black soil at Ellerslie and a Gray Luvisol at Breton. The total quantity of carbon in the system, of which soil C was the largest component, was less at Breton (6.6 $kg/m^2$) than at Ellerslie (17.2 $kg/m^2$). Soluble C, polysaccharide C, and microbial C showed similar trends. Despite a smaller microbial biomass the quantity of $CO_2$ - C ($g/m^2$) respired during 10-day incubation was up to 2 times greater at Breton than Ellerslie. The quantity of $CO_2$ - C released per gram of microbial biomass was 2 to 4 times greater at Breton than at Ellerslie. The proportion of soil C in microbial and soluble C pools was greater at Breton than Ellerslie. Because soluble C and microbial C have shorter turnover times than soil C as a whole, soil C was less stable at Breton than at Ellerslie.

There were no differences in activity between sites for any of the pools after pulse labelling except for the quantity of $^{14}C$ ($MBq/m^2$) in soil, which was 12 to 76 times greater at Breton than Ellerslie. At the time of labelling, the soil at Breton was visibly wet while the soil at Ellerslie was not; soluble C (g/g root C), a measure of root derived C in the soil, increased when water filled porosity exceeded 70%. Constant soil and microbial $^{14}C$ activities over the four sampling dates indicated a constant release of $^{14}C$ to the soil from root turnover. The specific activity of microbial C was lower than that of respired C, indicating that only part of the microbial biomass was active (17% at Ellerslie and 43% at Breton).

Overall, the carbon content of the system was lower at Breton than at Ellerslie and a larger proportion of soil C was in the less stable microbial and soluble pools. Even though there was less microbial biomass at Breton than Ellerslie, more C was respired on a microbial C basis and a greater proportion of the total microbial biomass was active.

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## Chapter 1. Introduction

Even though Gray Luvisols and Black soils occur in geographically adjacent areas transitional between grassland and boreal forest, relatively few comparative studies of these soils have been published. Both soils are of agricultural importance. Of the 80 M ha of Gray Luvisols in Canada 12 M ha are arable and 5.2 M ha are in agricultural use. There are 19 M ha of Black soils in Canada. Of these 16 M ha are arable and under agricultural production (Acton 1978). Under optimum management, surface crusting and inadequate nitrogen supply may result in yields of barley, oats, and canola on Gray Luvisols which are approximately two thirds of those obtained on Black soils although forage yields are often equal or better (Hoyt et al. 1978). Gray Luvisols must be managed more carefully than Black soils to maintain agricultural productivity (Bentley et al. 1971). Many of the soil related problems inherent to Gray Luvisols, such as poor soil structure, low fertility, low water holding capacity, and low buffering capacity are associated with low organic matter levels in the Ap horizon (Robertson and McGill 1983, Hoyt et al. 1978). Thus increasing organic matter levels should be one of the goals of agricultural management practices on Gray Luvisols.

Soil is the major resevoir for carbon in the terrestrial C cycle. Soil C is maintained by the balance between photosynthesis and decomposition (Goudriaan 1987). Any attempts to manipulate the mass of soil C in Black soils or Gray Luvisols will require a sound understanding of how carbon cycles in the two soils. Gray Luvisols and Black soils have developed a number of different characteristics pertaining to the cycling of carbon through the soil. There is less organic C in Gray Luvisols than in Black soils (Reinl 1984) and carbon turnover rates have been reported to be higher (Campbell et al. 1967). Organic matter in Gray Luvisols differs chemically from that in Black soils. The proportion of aromatic components and their degree of condensation have been reported to be less in the humic acids of

Black soils than in those of Gray Luvisols (Anderson et al. 1974). More $^{14}CO_2$ was respired from a Gray Luvisol than from a Black soil during laboratory incubations following the addition of $^{14}$C-glucose (Juma et al. 1984). The mineralization of carbon is also tied to the mineralization of nitrogen in soil (Stewart et al. 1983). Potentially mineralizable N makes up a larger proportion of total N in cultivated Gray Luvisols than in Black soils (Campbell and Souster 1982).

Differences in carbon cycling have implications for the agronomic management of the two soils. Maintainence of organic matter is more difficult in soils which mineralize a larger proportion of carbon additions. Crop yields tend to be greater on rotations which favour the accumulation of soil organic matter although no formal links have been established between organic matter and crop yield (Droeven et al. 1982, Johnston 1982). Soil organic matter may indirectly affect crop yields through its influence on soil fertility, stable soil structure, and water holding capacity but there may be more direct effects as well. When all other conditions such as N supply and soil moisture are equalized in greenhouse trials, crop yields are higher when straw or alfalfa residues are added to the soil than when no organic additions are made. The effect of organic residues is greatest on those soils which have the least organic C (Hedlin 1986).

With these observations in mind this study was initiated to investigate some of the differences in carbon cycling under field conditions between a Black soil and a Gray Luvisol, both of which were cropped to barley. Both conventional and tracer techniques were used. The objectives of this study were to construct a $^{12}$C budget for each site and study the allocation of carbon within the soil systems between microbial, water soluble and polysaccharide C pools. The plants were pulse labelled with $^{14}CO_2$ in order to observe differences in the allocation of photosynthetically fixed carbon between the two systems during the growing season. The results obtained are presented and discussed in two separate chapters,

one dealing with the $^{12}C$ data and the other with the $^{14}C$ data, followed by a synthesis and overall conclusions.

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## Chapter 2. Above and belowground allocation of $^{12}C$, distribution in soil, and microbial utilization[1]

### Introduction

Organic carbon dynamics do not follow the same pattern in Black soils and Gray Luvisols. Laboratory incubation studies showed that a larger percentage of added carbon is respired from a Gray Luvisol soil than from a Black soil (Juma et al. 1984). These soils also respond in different ways to agronomic practices such as tillage and crop rotation. Potentially mineralizable nitrogen makes up a smaller proportion of total nitrogen in virgin Gray Luvisols than in virgin Black soils while this trend is reversed after cultivation (Campbell and Souster 1982). The turnover of soluble amino acids is faster in cultivated than in virgin soils, and in a wheat-fallow rotation than in a five year rotation with two years of forage (Monreal 1987).

Differences in aboveground crop yield may be associated with these differences in carbon cycling. McGill et al. (1986) found that the rotation which maximized yield also had the highest soil C levels and slowest turnover through microbial biomass and soluble C pools. The quantity of carbon lost from roots has been reported to increase when microorganisms are present (Martin 1977). Rhizosphere microorganisms may affect the loss of carbon from roots by the production of phytohormones (Vancura and Jandera 1986) and by maintaining a concentration gradient which promotes the diffusion of soluble carbon from roots (Prikryl and Vancura 1980). Thus, microbial use of carbon may create an increased demand for carbon in the rhizosphere. If plants are unable to compensate for the loss of carbon from roots, crop yields may decrease (Ryle et al. 1979). An

[1]A version of this chapter has been submitted for publication to the Canadian Journal of Soil Science.

understanding of carbon cycling in different soils and the effects of agronomic practices on carbon cycling may aid in developing productive and efficient cropping systems for specific soils.

This study was undertaken to compare carbon cycling in a Gray Luvisol and a Black soil cropped to barley. Above and belowground allocation of carbon, distribution of carbon in soil, and microbial use of carbon were measured.

## Materials and methods

### Site Description:

This study was conducted at the Ellerslie Research Station located at NE 24-51-25 $W_4$, approximately 10 km southwest of the University of Alberta and at the University of Alberta Breton plots located at NE-25-47-4 $W_5$, 110 km southwest of Edmonton. Ellerslie receives an average of 452 mm of precipitation annually of which 339 mm occurs as rain and 113 mm occurs as snow. Breton receives 547 mm of precipitation during the year with 405 mm of rain and 132 mm of snow. The months of greatest rainfall are June, July, and August and the greatest snowfall occurs during December and January at both sites. July is the warmest month at both sites with an average minimum temperature of 9.6 °C at Ellerslie and 8.8 °C at Breton and a maximum of 22.4 °C at Ellerslie and 21.2 °C at Breton. January is the coldest month with average minimum temperatures of -21.7 °C at Ellerslie and -19.5 at Breton and average maximum temperatures of -11.5 °C at Ellerslie and -8.6 °C at Breton. Ellerslie has an average of 109 frost free days per year and Breton an average of 80. Black soils are dominant at Ellerslie (Bowser et al. 1962) while Gray Luvisols complexed with Dark Gray Luvisols are dominant at Breton (Lindsay et al. 1968). Some soil properties are given in Table II.1.

Table II.1. Soil properties at Ellerslie and Breton.

| Depth (cm) | Carbon (%) | Nitrogen (%) | pH (1:2 soil:water) (w/v) | Bulk Density ($Mg\ m^{-3}$) |
|---|---|---|---|---|
| **Ellerslie** (Black; Typic Cryoboroll) | | | | |
| 0-10 | 6.5 | 0.53 | 6.1 | 0.85 |
| 10-20 | 6.3 | 0.49 | 6.0 | 1.06 |
| 20+ | 5.2 | 0.42 | 6.0 | 1.16 |
| **Breton** (Gray Luvisol; Typic Cryoboralf) | | | | |
| 0-10 | 2.2 | 0.18 | 6.2 | 1.10 |
| 10-20 | 1.9 | 0.16 | 6.3 | 1.30 |
| 20+ | 1.1 | 0.10 | 6.1 | 1.55 |

The area on which the plots were established at Ellerslie was in a bromegrass (*Bromus inermis* L.) - alfalfa (*Medicago sativa* L.) forage mix from 1971 to 1984, broken in the fall of 1984 and seeded to barley in 1985. The plot area at Breton was in barley (*Hordeum vulgare* L.) or fallow from 1972 until 1986. Both sites were fertilized with urea-N (77.3 kg/ha) and treble superphosphate-P (47.2 kg/ha) and seeded to barley (cv. Empress) in the spring of 1986. No herbicides were used during the study.

**Sampling Procedure:**

Four steel cylinders, 20 cm in diameter by 30 cm in depth, were installed in each of the three replicates of barley plots (24.7 m x 9.3 m at Ellerslie and 12 m x 6.8 m at Breton). Barley (*Hordeum vulgare* L. cv. Empress) was sown into the microplots on May 28 (day 148), 1986 at the rate of 8 seeds per cylinder. Microplots were used so the plants could be labelled with $^{14}CO_2$ in July.

The microplots were sampled on July 31 (day 212), August 18 (day 230), September 8 (day 251), and September 29 (day 272) at Ellerslie, and August 11 (day 223), September 1 (day 244), September 22 (day 265), and October 20 (day

293) at Breton. The final sampling date at Breton was delayed due to wet conditions which prevented access to the field.

At each sampling date shoot material was harvested from one cylinder in each replicate and the cylinder was then removed from the field. The soil in the cylinder was divided into three depths: 0 - 10 cm, 10 - 20 cm, 20 + cm. Roots were separated manually from the soil. Soil samples were stored moist at 5°C.

**Analyses:**

Shoot and root materials were dried at 70°C and weighed. Dry shoot material was ground to 20 mesh with a Wiley mill. Dried root material and a subsample of air dried soil from each depth were ground in a mortar and pestle. Total carbon was determined on ground plant and soil subsamples by dry combustion using a Leco Carbon Determinator CR-12. Carbon content in roots was determined only for the 0 - 10 cm depth because of the small quantity of root material below 10 cm. The amount of root C below 10 cm was calculated by multiplying the measured root mass by the carbon concentration determined for roots in the 0 - 10 cm depth.

Microbial respiration and microbial biomass C were measured on 25-g samples of moist (55% water holding capacity), seived soil by the chloroform fumigation technique (Jenkinson and Powlson 1976). $CO_2$-C released during incubation was trapped gravimetrically in 0.25 M NaOH. The flush of $CO_2$-C from the decomposition of microbial cells was calculated as the difference between the amount of $CO_2$-C released during a 10-day incubation after fumigation and that released during the same period from unfumigated samples. Microbial biomass C was calculated by dividing the flush of $CO_2$-C by a $K_c$ factor of 0.411 (Anderson and Domsch 1978). The quantity of $CO_2$-C released by the unfumigated samples during the 10-day incubation was used as a measure of microbial respiration.

Water soluble organic carbon was determined using the method of McGill et al. (1986). A 10-g sample of field moist soil was shaken in 20 mL of distilled water for one hour, centrifuged, and filtered through a 0.45 µm Millipore filter. The extract was frozen until analysis on a Beckman Total Organic Carbon Analyser, Model 915-B.

Polysaccharide carbon was extracted after the method of Cheshire and Mundie (1966). A 1-g air dry sample was hydrolysed in 12 M $H_2SO_4$ at room temperature for 16 hours then diluted to 0.5 M and hydrolysed at 100°C for a further 4 hours. The hydrolysate was filtered through a glass fibre filter and 5 M NaOH was added until a precipitate formed. A subsample of the hydrolysate plus precipitate was centrifuged to remove the precipitate and the solution retained for determination of the reducing sugar content by the reduction of alkaline ferricyanide using glucose as a standard (Friedemann et al. 1962).

**Statistical analyses:**

The design was a factorial split-plot with 3 replicates per site. The data were analysed using the UANOVA multivariate analysis of covariance program developed at the University of Alberta (Taerum submitted). This procedure gives the usual F ratio found in an ANOVA table as well as an F ratio which has been adjusted for unequal variances of the means by the Greenhouse-Geisser adjustment (Greenhouse and Geisser 1959). Probabilities derived from the Greenhouse-Geisser adjusted F ratios have been used in the following results. When a significant F ratio was found the sums of squares for that source of variation were partitioned into single degree of freedom effects as recommended in Mize and Schultz (1985).

**Results**

Differences in the carbon content of shoots, roots, microbial biomass, and soil over the four sampling dates were not significant (Table II.2). Shoot C at Ellerslie was up to 2.8 times greater than at Breton (p= 0.0431). Root C did not differ between sites but decreased with depth (p=0.0001). Microbial biomass C was 1.5 to 2.5 times greater at Ellerslie than at Breton (p=0.0020) and varied with depth (p=0.0060) with more microbial C in the 0 - 10 and 10 - 20 cm depths than the 20 + cm depth. Soil C was 2.5 to 3.5 times higher at Ellerslie than Breton (p=0.0001) and changed with depth (p=0.0010). A site by depth interaction was found (p=0.0429) and further analysis showed that the distribution of soil C with depth followed a quadratic trend (Fig. II.1(1a)). It was highest in the 10 - 20 cm depth and lowest in the 20 + cm zone with a greater difference between depths at Ellerslie than at Breton. The total C content of the system was 2.5 to 3 times greater at Ellerslie than Breton (p=0.0001).

Shoot C/root C ratios (p=0.0115) and microbial biomass C/root C ratios (p=0.0198) were both up to 2 times greater at Ellerslie than Breton (Table II.3). The quantity of $CO_2$-C released during 10-day incubation (mg/g microbial C) was 2 to 5 times higher at Breton than Ellerslie (p=0.0022) (Table II.3). Changes in ratios of shoot C/root C, microbial biomass C/root C or respired C/microbial biomass C over time were not significant. When expressed on an area basis, the amount of $CO_2$-C ($mg/m^2$) released from soil samples during laboratory incubation was up to 2 times higher at Breton than Ellerslie (p=0.0075) and varied over the four sampling dates (p=0.0274) (Table II.3). A site by date interaction occurred (p=0.0206) which followed a quadratic trend where respired carbon at Breton increased with time then decreased while at Ellerslie respiration decreased initially and then increased (Fig. II.1(1b)).

Table II.2. C budget (g C/m$^2$) in the plant-soil system at Ellerslie and Breton.

| Compartment | Depth(cm) | Day of the year§ 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|---|
| | | **Ellerslie** | | | |
| **Shoot** | | 119.5 | 235.6 | 365.5 | 266.1 |
| **Root** | 0 - 10 | 19.7 | 12.5 | 13.3 | 19.7 |
| | 10 - 20 | 3.0 | 3.2 | 5.3 | 4.0 |
| | 20 + | 1.3 | 1.5 | 2.1 | 2.5 |
| **Microbial C** | 0 - 10 | 48.8 | 38.3 | 52.8 | 44.0 |
| | 10 - 20 | 47.8 | 51.4 | 44.7 | 47.4 |
| | 20 + | 15.5 | 23.6 | 22.7 | 27.0 |
| **Soil** | 0 - 10 | 5626 | 5147 | 5778 | 5565 |
| | 10 - 20 | 7100 | 6719 | 6613 | 6395 |
| | 20 + | 4643 | 4464 | 4468 | 4872 |
| **Total** | | 17705 | 16696 | 17366 | 17198 |
| | | **Breton** | | | |
| **Shoot** | | 163.3 | 166.1 | 162.1 | 95.2 |
| **Root** | 0 - 10 | 15.8 | 21.9 | 18.0 | 15.9 |
| | 10 - 20 | 2.1 | 1.5 | 1.8 | 2.0 |
| | 20 + | 0.3 | 0.4 | 0.2 | 0.3 |
| **Microbial C** | 0 - 10 | 22.6 | 26.9 | 32.6 | 23.3 |
| | 10 - 20 | 27.1 | 16.0 | 22.0 | 26.8 |
| | 20 + | 13.0 | 15.0 | 14.9 | 15.8 |
| **Soil** | 0 - 10 | 2418 | 2344 | 2411 | 2329 |
| | 10 - 20 | 2483 | 2781 | 2221 | 2490 |
| | 20 + | 1409 | 1775 | 1217 | 1514 |
| **Total** | | 6555 | 7148 | 6080 | 6511 |

**Summary of analysis of variance**

| Source of Variation | Shoot C | Root C | Microbial C | Soil C | Total C |
|---|---|---|---|---|---|
| Site | * | ns | ** | *** | *** |
| Date | ns | ns | ns | ns | ns |
| Site x Date | ns | ns | ns | ns | ns |
| Depth | | *** | ** | *** | |
| Site x Depth | | ns | ns | * | |
| Date x Depth | | ns | ns | ns | |
| Site x Date x Depth | | ns | ns | ns | |

In this and all subsequent tables:

§ - sampling date for Ellerslie and Breton respectively, microplots were seeded on day 148.

The difference between means is significant at: ns, not significant; *, adjusted $p<0.05$; **, adjusted $p<0.01$; ***, adjusted $p<0.001$.

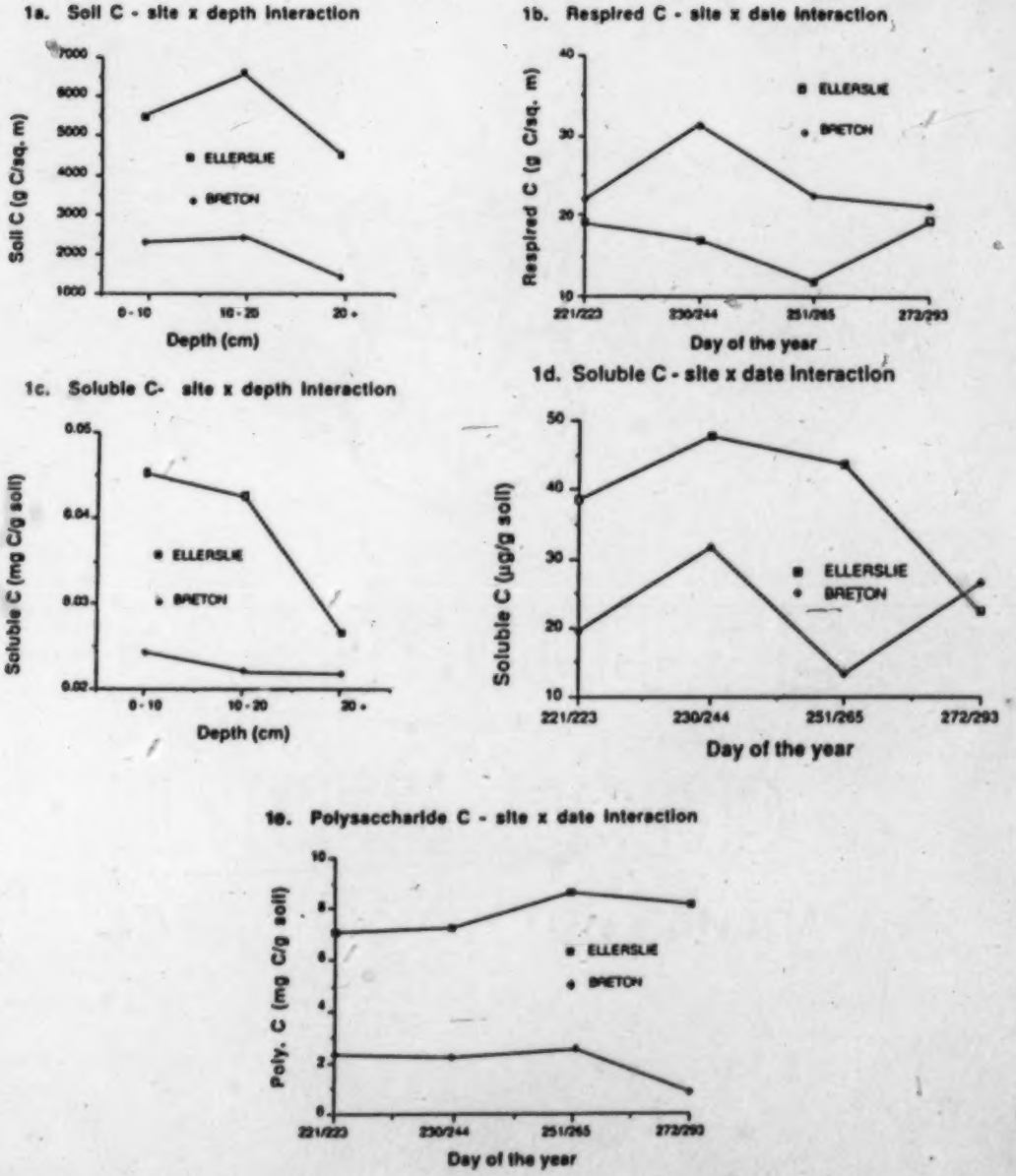


**Figure II.1 Selected site by depth and site by date interactions at Ellerslie and Breton.**

Table II.3. Pool size ratios at Ellerslie and Breton.

| Ratio | Day of the year 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|
| | | **Ellerslie** | | |
| Shoot C/Root C | 8.0 | 13.5 | 17.6 | 10.4 |
| Microbial C/Root C | 5.1 | 6.6 | 5.9 | 4.6 |
| $CO_2$-C/Microbial C† | 0.17 | 0.15 | 0.10 | 0.17 |
| $CO_2$-C($g/m^2$)† | 19.3 | 17.1 | 11.8 | 19.5 |
| | | **Breton** | | |
| Shoot C/Root C | 9.1 | 6.8 | 8.8 | 5.6 |
| Microbial C/Root C | 3.8 | 2.5 | 2.8 | 4.5 |
| $CO_2$-C/Microbial C† | 0.36 | 0.58 | 0.48 | 0.33 |
| $CO_2$-C($g/m^2$)† | 21.9 | 31.2 | 22.6 | 21.3 |

**Summary of analysis of variance**

| Source of Variation | Shoot C/ Root C | Microbial C/ Root C | $CO_2$/ Microbial C | $CO_2$/ $m^2$ |
|---|---|---|---|---|
| Site | * | * | ** | ** |
| Date | ns | ns | ns | * |
| Site x Date | ns | ns | ns | * |

† - $CO_2$-C evolved from unfumigated 10-day incubation

Microbial biomass C on a total soil mass basis was 2 to 4 times higher at Ellerslie than Breton (p=0.0007) (Table II.4) but when expressed on a mass of soil C basis it was 1.3 times higher at Breton (p=0.0473) (Table II.5). When expressed either way, microbial biomass decreased linearly with depth (p=0.0010 on a per gram soil basis, p=0.0413 on a per gram soil C basis). Because no differences over time were significant, the values presented in Table II.5 are means of the four sampling dates.

Soluble C(μg was up to 4 times greater at Ellerslie than Breton (p=0.0044) and decreased linearly with depth (p=0.0153) (Table II.4). There was also a

Table II.4. Microbial biomass C, water soluble organic C, and polysaccharide C at Ellerslie and Breton.

| Depth (cm) | Day of the year 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|
| | **Microbial C (mg/g soil)** | | | |
| | | Ellerslie | | |
| 0 - 10 | 0.55 | 0.47 | 0.59 | 0.52 |
| 10 - 20 | 0.44 | 0.47 | 0.43 | 0.47 |
| 20 + | 0.18 | 0.28 | 0.25 | 0.30 |
| | | Breton | | |
| 0 - 10 | 0.21 | 0.23 | 0.25 | 0.22 |
| 10 - 20 | 0.21 | 0.13 | 0.11 | 0.21 |
| 20 + | 0.09 | 0.11 | 0.07 | 0.12 |
| | **Water soluble organic C (mg/g soil)** | | | |
| | | Ellerslie | | |
| 0 - 10 | 0.044 | 0.058 | 0.053 | 0.026 |
| 10 - 20 | 0.043 | 0.052 | 0.050 | 0.025 |
| 20 + | 0.029 | 0.034 | 0.028 | 0.016 |
| | | Breton | | |
| 0 - 10 | 0.018 | 0.036 | 0.014 | 0.030 |
| 10 - 20 | 0.019 | 0.030 | 0.012 | 0.028 |
| 20 + | 0.022 | 0.029 | 0.014 | 0.022 |
| | **Polysaccharide C (mg/g soil)** | | | |
| | | Ellerslie | | |
| 0 - 10 | 8.2 | 8.9 | 9.9 | 9.4 |
| 10 - 20 | 6.6 | 6.4 | 9.0 | 8.9 |
| 20 + | 0.2 | 6.5 | 7.4 | 6.5 |
| | | Breton | | |
| 0 - 10 | 2.9 | 2.9 | 3.2 | 1.5 |
| 10 - 20 | 2.6 | 2.2 | 2.5 | 0.7 |
| 20 + | 1.1 | 1.4 | 1.4 | 0.1 |

**Summary of analysis of variance**

| Source of Variation | Microbial C | Soluble C | Polysaccharide C |
|---|---|---|---|
| Site | *** | ** | *** |
| Date | ns | * | ns |
| Site x Date | ns | * | * |
| Depth | *** | * | ** |
| Site x Depth | ns | * | ns |
| Date x Depth | ns | ns | ns |
| Site x Date x Depth | ns | ns | ns |

Table II.5. Microbial biomass, water soluble organic and polysaccharide C per g soil C at Ellerslie and Breton.

| Depth (cm) | Microbial C (mg/g soil C) | Soluble C (mg/g soil C) | Polysaccharide C (mg/g soil C) |
|---|---|---|---|
| | | **Ellerslie** | |
| 0 - 10 | 8.2 | 0.70 | 141 |
| 10 - 20 | 7.2 | 0.68 | 122 |
| 20 + | 4.8 | 0.51 | 128 |
| | | **Breton** | |
| 0 - 10 | 10.5 | 1.14 | 122 |
| 10 - 20 | 8.6 | 1.14 | 108 |
| 20 + | 7.6 | 2.26 | 98 |

**Summary of analysis of variance**

| Source of Variation | Microbial C | Soluble C | Polysaccharide C |
|---|---|---|---|
| Site | * | * | ns |
| Date | ns | ns | ns |
| Site x Date | ns | ns | ns |
| Depth | * | ns | ns |
| Site x Depth | ns | ns | ns |
| Date x Depth | ns | ns | ns |
| Site x Date x Depth | ns | ns | ns |

significant (p=0.0160) site by depth interaction caused by the fact that the concentration of soluble C/g soil showed a greater linear decrease with depth at Ellerslie than at Breton (Fig. II.1(1c)). Soluble C varied over the four sampling dates and the pattern of this variation differed between sites, causing a significant site by date interaction (p=0.0160) (Fig. II.1(1d)). When expressed on a per gram soil C basis, soluble C at Breton was 1.5 to 4.5 times higher than at Ellerslie (p=0.0445) and no significant differences were observed between depths (Table II.5).

Polysaccharide C/g of soil was 2 to 5 times greater at Ellerslie than at Breton (p=0.0001) and decreased with depth (p=0.0040), following a linear trend

(p=0.0001) (Table II.4). There was also a significant site by date (p=0.0434) interaction indicating that polysaccharide C showed a general linear increase over time at Ellerslie but decreased at Breton (Fig. II.1(1e)). When expressed on a per gram soil C basis there was no difference between sites or depths (Table II.5).

## Discussion

### Above and belowground carbon allocation

The amount of carbon allocated to shoot production was lower at Breton than Ellerslie while carbon allocated to root production at the two sites was similar resulting in lower shoot C/root C ratios at Breton. This could have been caused by aboveground environmental conditions such as temperature and light, or by soil conditions such as moisture status, available nitrogen, and temperature (Hunt and Lloyd 1987). Soil bulk density was greater at Breton than Ellerslie but this tends to affect root and shoot mass equally, resulting in no change to shoot/root ratios (Goss 1977). Temperatures at Breton tended to be slightly lower than at Ellerslie but the effect of temperature on shoot/root ratios is difficult to predict because the difference between root and shoot temperature is of more consequence to shoot/root partitioning than is the overall temperature (Davidson 1969). During the month of July Breton received a larger amount of precipitation (283 mm) than Ellerslie (126 mm) which caused waterlogged soil conditions for at least part of July. Waterlogging itself could not have caused lower shoot/root ratios at Breton because anaerobic soil conditions increase shoot/root ratios (Trought and Drew 1980) however, waterlogging at Breton may have caused a loss of available nitrogen due to leaching and/or denitrification. The nitrogen content of shoots at head emergence was 2.50% at Ellerslie and 0.71% at Breton (P. M. Rutherford, personal communication). Shoot N content at Breton was deficient (Ward et al. 1973) but

was sufficient at Ellerslie. Shoot/root ratios are known to decrease in response to nitrogen deficiency (Brouwer 1983) and stress in the root environment may have greater consequences for plant growth and shoot/root partitioning than stress in the shoot environment (Hunt and Nicholls 1986). Excess moisture and its effect on available nitrogen may have been the major factor affecting carbon partitioning in barley plants at the two sites.

**Microbial use of root carbon**

The similarity in root mass at both sites was not reflected in the quantity of microbial C because there was less microbial C at Breton than Ellerslie. Microbial C/g of root C was also lower at Breton than Ellerslie indicating that factors other than standing root mass determined the quantity of microbial C. The difference in microbial C at the two sites may not be due to any restriction in the availability of root C because the quantity of $CO_2$ released from soil during a laboratory 10-day incubation, expressed on an area basis, was greater at Breton than Ellerslie. Instead, it appears that the smaller microbial biomass at Breton was due to a difference in the metabolism of the microorganisms at the two sites. The quantity of $CO_2$ released per g of microbial biomass C was 2 to 4 times higher at Breton than at Ellerslie indicating that, in proportion to the quantity of microbial C, more of the carbon was lost through respiration at Breton. Thus, less microbial C was maintained per unit of available carbon. Juma et al. (1984) also found more $^{14}CO_2$ was released from a Gray Luvisol than a Black soil following the addition of $^{14}C$-glucose.

Cropping history may also have affected respiration rates. The plots at Ellerslie had been in bromegrass-alfalfa from 1971 until 1985, while at Breton the plots had been in barley or fallow. McGill et al. (1986) found that microbial biomass turnover in a 2-year wheat-fallow rotation at Breton was faster than in a 5-

year rotation which included forages. Monreal (1987) found turnover of amino acids through the soluble pool, which is the main source of substrate for bacteria in the rhizosphere (Newman 1985), was also faster in the same 2-year wheat-fallow rotation than in the 5-year rotation and faster in three cultivated Chernozems than in a corresponding virgin Chernozem. Cropping history at Breton may have stimulated microbial biomass to greater respiratory activity than at Ellerslie.

**Distribution of carbon within the soil system**

Expression of microbial C, soluble C, and polysaccharide C on a per gram soil C rather than a per g soil basis gives a different picture of the carbon economy of the two sites. Even though the quantity of microbial biomass per g of soil was lower at Breton than Ellerslie, the quantity of microbial biomass C per g of soil C was higher. This trend was reflected for soluble C as well. The quantity of polysaccharide C per g of soil C was the same at both sites.

Microbial biomass C, soluble C, polysaccharide C, and soil organic C each represent kinetically distinct pools of the soil carbon cycle. Turnover times have been estimated to be 0.026 to 0.038 yr for soluble C (McGill et al. 1986), 0.26 to 5 yr for microbial biomass (McGill et al. 1986), 0.17 to 5.26 yr for polysaccharide C (Murayama 1984), and 5.7 to 900 yr for stabilized and old organic matter respectively (Juma and Paul 1981). Soil organic C is the largest, most stable pool in the soil system. By expressing the other carbon pools in terms of soil C, the distribution of carbon between these kinetically defined pools may be compared on a relative basis. The amount of polysaccharide C as a proportion of soil C was statistically similar at the two sites however a larger proportion of the carbon at Breton was in the microbial biomass C and in the soluble C pools (Table II.5). The latter have higher turnover rates than soil organic matter as a whole, therefore less of the belowground carbon at Breton was stable. Campbell and Souster (1982)

have observed a similar distribution of nitrogen in Luvisolic and Chernozemic soils. Potentially mineralizable nitrogen made up a larger proportion of total nitrogen in cultivated Gray Luvisols than in cultivated Black soils. Soil texture, which was coarser at Breton (L) than at Ellerslie (SiCL), may also have reduced carbon stabilization at Breton. In several soils, which covered a range of soil textures, potentially mineralizable nitrogen as a percentage of total nitrogen increased as soil texture became coarser (Campbell and Souster 1982).

## Conclusions

When compared with Ellerslie, the system at Breton was characterized by less C in the soil, more C respired by soil microorganisms relative to the quantity of microbial C in the soil, and a greater proportion of C in soil pools with short turnover times. Pedogenic characteristics may have contributed to the difference between sites in carbon distribution and microbial use of carbon. Organic carbon and nitrogen in Luvisolic soils appears to be less stable and the microbial biomass more active than in Chernozemic soils. Cropping history, which was different at Breton than Ellerslie, may also have caused site differences. The implication of these differences in carbon cycling to soil organic matter and crop yields should be considered when designing cropping systems appropriate to specific areas.

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## Chapter 3. Factors affecting the distribution and dynamics of $^{14}C$[2].

### Introduction

A number of differences in soil characteristics between Black and Gray Luvisolic soils point to differences in carbon cycling. Black soils have 3 to 5 times more organic carbon than Gray Luvisols (Reinl 1984). The organic matter in Black soils differs chemically from Gray Luvisols (Anderson et al. 1974) and turnover of organic carbon has been reported to be slower (Campbell et al. 1967). Juma et al. (1984) found that more $^{14}CO_2$ was released after the addition of $^{14}C$-glucose from a Gray Luvisol than a Black soil.

Agronomic management may also affect carbon cycling. McGill et al. (1986) reported turnover of microbial and soluble C under field conditions was faster in a wheat-fallow rotation than in a 5-year rotation with 3 years of cereals and 2 years of forage at the University of Alberta Breton plots. Monreal (1987) found turnover of soluble amino acids under laboratory conditions was faster in soil samples from the same wheat-fallow rotation than in the 5-year rotation.

Other environmental and soil conditions may influence the cycling of carbon. The input of carbon from plant roots during the growing season is affected by factors such as soil moisture (Martin 1977b, Wiedenroth and Poskuta 1981), plant nutrient status (Trolldenier 1979), and temperature (Martin 197[illegible] Turnover of root carbon was reported to be faster in sandy soils than in clay soils (Merckx et al. 1985), wetting and drying cycles affect the decomposition of organic material (van Veen et al. 1984), and soil aeration influences the biochemical pathways and fate of carbon in soil (Novak 1983, Linn and Doran 1984).

[2]A version of this chapter has been submitted for publication to Plant and Soil.

The objective of this study was to evaluate carbon cycling in a barley crop grown under field conditions on two pedogenically different soils, a Gray Luvisol and a Black soil. $^{12}C$ distribution and the distribution and the dynamics of $^{14}C$ in the various plant and soil pools was measured after pulse labelling with $^{14}CO_2$.

## Materials and methods

### Site Description:

The sites and soil characteristics have been described in detail in Chapter 2 and Table II.1.

### Labelling Procedure:

Four microplots made of steel cylinders, 20 cm in diameter by 30 cm in depth, were installed in each of the three replicates of barley plots (24.7 m x 9.3 m at Ellerslie and 12 m x 6.8 m at Breton). Barley (cv. Empress) was sown into the microplots on May 28, 1986 at the rate of 8 seeds per cylinder. Plants were labelled with $^{14}CO_2$ between flag leaf and swollen boot stages (July 21 at Ellerslie, July 31 at Breton). Labelling was delayed at Breton due to wet conditions which prevented access to the field. Clear plastic canopies, sealed to the tops of the cylinders with large hose clamps over foam rubber strips, were used to enclose the plants. A test tube was sealed into the top of each canopy so that the top of the tube remained outside the canopy while the body of the tube was inside the canopy. A solution of $Na_2{}^{14}CO_3$ was placed in each test tube and $^{14}CO_2$ was released through a hole in the body of the tube by injecting lactic acid through a rubber serum cap in the mouth of the tube. Each cylinder received 3.7 MBq $^{14}C$. A two hour labelling period was used and 3mL $^{12}CO_2$ were added after 30 to 40 minutes to maintain the photosynthetic rate. At the end of the labelling period NaOH was injected through a rubber serum cap into a beaker held within the canopy in order to absorb the $CO_2$ remaining in the canopy atmosphere before the canopies were removed. A small

battery operated fan was enclosed in each canopy to ensure complete mixing of the air.

**Sampling Procedure:**

The plots were sampled as described in Chapter 2.

**Analyses:**

Gravimetric soil moisture was measured on duplicate samples (approximately 10 g) taken from each depth and weighed before and after drying at 105 °C. Water filled porosity = $\theta_v$/TP was determined for each sampling date where $\theta_v$ = volumetric moisture content = $\theta_m$(Db), $\theta_m$ = gravimetric moisture (Mg/Mg), TP = total porosity = (1-(Db/Dp)), Db = bulk density (Mg/m$^3$) and Dp= particle density (assumed to be 2.65 Mg/m$^3$). Water filled porosity was chosen as a measure of soil moisture content since gravimetric moisture did not adequately describe the differences in soil moisture between the two sites due to differences in bulk density, texture and structure.

Sample preparation and the methods used for the measurement of $^{12}C$ in shoot, root, and soil samples have been described in Chapter 2. The quantity of $^{14}C$ in shoots, roots, and soil was determined after oxidation in a Harvey Biological Oxidizer, Model OX300. $^{14}C$ released during oxidation was trapped in Harvey's $^{14}C$ Cocktail and measured with a Minaxiß Tri-Carb 4000 series scintillation counter.

Microbial respiration and microbial biomass C was measured by the chloroform fumigation technique (Jenkinson and Powlson 1976) as described in Chapter 2. Aliquots of 0.25M NaOH (0.5mL) containing trapped $CO_2$ from either the fumigated or unfumigated treatments were added to Scintiverse 1 (15mL) and analysed for $^{14}C$ on a Searle Isocap 300 scintillation counter.

Water soluble organic carbon was determined using the method of McGill et al. (1986) as described in Chapter 2.

**Statistical analyses:**

The data were analysed using the UANOVA multivariate analysis of covariance program developed at the University of Alberta (Taerum submitted) as described in Chapter 2.

**Results**

The quantity of $^{12}C$ found in shoots, roots, and soil over the four sampling dates has been described in Chapter 2 (Table II.2).

The quantity of $CO_2$-C ($mg/m^2$) respired from fumigated samples was approximately 1.5 times greater at Ellerslie than Breton ($p=0.0186$) and decreased linearly with depth ($p=0.0005$) (Table III.1). There were no significant differences between sampling dates. As described in Chapter 2, the amount of $CO_2$-C respired from unfumigated samples was up to 2 times higher at Breton than Ellerslie ($p=0.0075$) and varied over the four sampling dates ($p=0.0274$) (Table III.1). The site by date interaction ($p=0.0206$) followed a quadratic trend showing similar respiration at both sites on the first and last sampling dates but different rates on the second and third samplings (Fig. II.1(1b)). Respiration was higher at Breton but lower at Ellerslie on the intermediate dates. Microbial biomass C, as determined by the chloroform fumigation technique, was 1.5 to 2.5 times greater at Ellerslie than at Breton ($p=0.0020$) and varied with depth ($p=0.0060$) with more microbial C in the 0 - 10 and 10 - 20 cm depths than the 20 + cm depth (Table III.1). There were no significant differences between sampling dates.

Unusually high rainfall resulted in waterlogged conditions within the microplots at Breton for some time prior to labelling. Normal rainfall during July is 84.5 mm at Ellerslie and 94.5 mm at Breton however during July 1986, Ellerslie received 1.5 times the normal rainfall while Breton received 3 times the normal. In the two weeks prior to labelling 244 mm of rain fell at Breton while 82 mm fell at

Table III.1. $CO_2$-C from fumigated and unfumigated incubations over 10 days and microbial biomass C at Ellerslie and Breton.

| Depth (cm) | Day of the year§ 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|
| | **Fumigated ($g/m^2$)** | | | |
| | **Ellerslie** | | | |
| 0 - 10 | 32.1 | 25.1 | 29.9 | 29.4 |
| 10 - 20 | 25.6 | 26.9 | 21.6 | 25.1 |
| 20 + | 14.0 | 11.6 | 9.8 | 13.7 |
| | **Breton** | | | |
| 0 - 10 | 20.7 | 23.8 | 23.9 | 20.1 |
| 10 - 20 | 18.3 | 18.6 | 16.7 | 17.7 |
| 20 + | 9.3 | 14.0 | 10.5 | 10.5 |
| | **Unfumigated ($g/m^2$)** | | | |
| | **Ellerslie** | | | |
| 0 - 10 | 12.0 | 9.4 | 8.2 | 11.3 |
| 10 - 20 | 5.9 | 5.8 | 3.2 | 5.6 |
| 20 + | 1.4 | 1.9 | 0.4 | 2.6 |
| | **Breton** | | | |
| 0 - 10 | 11.4 | 12.8 | 10.5 | 10.5 |
| 10 - 20 | 7.1 | 10.6 | 7.6 | 6.7 |
| 20 + | 3.4 | 7.8 | 4.4 | 4.0 |
| | **Microbial C ($g/m^2$)** | | | |
| | **Ellerslie** | | | |
| 0 - 10 | 48.8 | 38.3 | 52.8 | 44.0 |
| 10 - 20 | 47.8 | 51.4 | 44.7 | 47.4 |
| 20 + | 15.5 | 23.6 | 22.7 | 27.0 |
| | **Breton** | | | |
| 0 - 10 | 22.6 | 26.9 | 32.6 | 23.3 |
| 10 - 20 | 27.1 | 16.0 | 22.0 | 26.8 |
| 20 + | 13.0 | 15.0 | 14.9 | 15.8 |

**Summary of analysis of variance**

| Source of Variation | Fumigated C | Unfumigated C | Microbial C |
|---|---|---|---|
| Site | * | ** | ** |
| Date | ns | * | ns |
| Site x Date | ns | * | ns |
| Depth | ** | *** | ** |
| Site x Depth | ns | ns | ns |
| Date x Depth | ns | ns | ns |
| Site x Date x Depth | ns | ns | ns |

In this and all subsequent tables:
§ - sampling date for Ellerslie and Breton respectively
The difference between means is significant at: ns, not significant; *, adjusted $p<0.05$; **, adjusted $p<0.01$; ***, adjusted $p<0.001$.

Table III.2. Water filled porosity and soluble organic C at Ellerslie and Breton.

| Depth (cm) | Day of the year 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|
| | **Water filled porosity (%)** | | | |
| | | **Ellerslie** | | |
| 0 - 10 | 43.9 | 18.3 | 17.4 | 48.9 |
| 10 - 20 | 54.4 | 37.1 | 29.7 | 59.4 |
| 20 + | 53.9 | 40.1 | 46.3 | 76.0 |
| | | **Breton** | | |
| 0 - 10 | 49.2 | 29.6 | 50.4 | 55.2 |
| 10 - 20 | 58.6 | 50.1 | 55.9 | 68.5 |
| 20 + | 86.8 | 86.6 | 90.0 | 80.0 |
| | **Soluble organic C** (g C/g root C) | | | |
| | | **Ellerslie** | | |
| 0 - 10 | 0.2 | 0.4 | 0.4 | 0.1 |
| 10 - 20 | 1.8 | 2.0 | 1.1 | 0.6 |
| 20 + | 2.0 | 2.4 | 1.4 | 0.6 |
| | | **Breton** | | |
| 0 - 10 | 0.1 | 0.2 | 0.1 | 0.2 |
| 10 - 20 | 2.3 | 2.7 | 1.6 | 2.2 |
| 20 + | 9.0 | 16.3 | 11.7 | 23.8 |

**Summary of analysis of variance**

| Source of Variation | Water filled porosity | Soluble C |
|---|---|---|
| Site | ** | * |
| Date | ** | ns |
| Site x Date | * | ns |
| Depth | *** | $ |
| Site x Depth | ns | ns |
| Date x Depth | ns | ns |
| Site x Date x Depth | ns | ns |

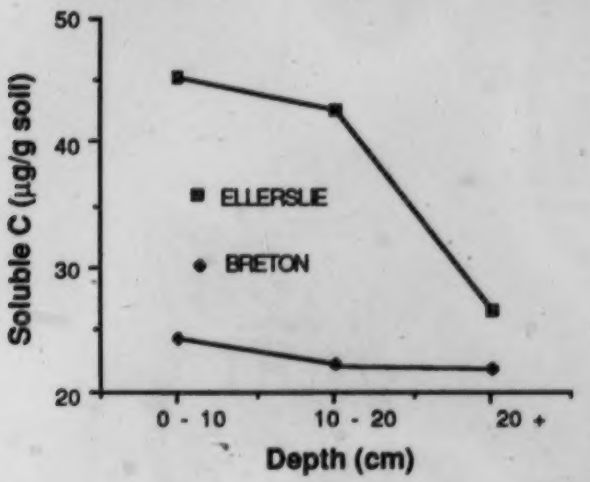
$ - difference between the means significant at an adjusted $p<0.010$.

Ellerslie. No soil moisture data were taken at the time of labelling but the soil at Ellerslie appeared to be at or below field capacity while the soil at Breton was visibly wet. Water filled porosity on the four sampling dates (Table III.2) was up to 3 times higher at Breton than Ellerslie ($p=0.0070$) and increased linearly with depth ($p=0.0001$). Water filled porosity also changed over time ($p=0.0005$). It was highest on the first and last sampling dates with differences between dates

being greater at Ellerslie than Breton, resulting in a site by date interaction (p=0.0435) which was quadratic (Fig. III.1(1a)).

The results of water soluble organic C (mg/g soil) measurements at Ellerslie and Breton were described in Chapter 2 (Table II.4). Soluble C (g/g root C) was used to estimate the quantity of root derived carbon in the soil on each sampling date (Table III.2). Overall, soluble C (g/g root C) was higher (up to 38 times) at Breton than Ellerslie (p=0.0541) and increased linearly with depth at both sites (p=0.0629). Soluble C (g/g root C) increased at high water filled porosities (Fig. III.2(2a)). Data from Ellerslie was not included in this relationship since water filled porosity was not high enough at any time to reveal the effect of high water filled porosity on soluble C (g/g root C). The ACE method of estimating optimum transformations (Breiman and Freidman 1985a) was used to examine the relationship between soluble C (g/g root C) and water filled porosity. The normal range for water filled porosity is 0 to 1.0, however there were a few points above 1.0. This may be due to errors encountered during measurement of bulk density or gravimetric moisture content. When transformed data obtained from this procedure are plotted against the untransformed data an abrupt change in slope indicates a separation between two groups of data points (Breiman and Freidman 1985b). The point at which the slope changes indicates the point of separation. A plot of transformed water filled porosity against untransformed data from Breton revealed a change in slope at about 70% water filled porosity (Fig. III.2(2b)). Since the transformed water filled porosity values are obtained from the relationship between soluble C and water filled porosity, both of which are entered into the ACE program at the same time, this change of slope at 70% water filled porosity indicates a change in the relationship between the two variables. At values above 70% water filled porosity the quantity of soluble C (g/g root C) was greater than the quantity found below 70%.

1a. Soluble C - site x depth interaction




1b. Unfumigated $CO_2$ specific activity - site by depth interaction

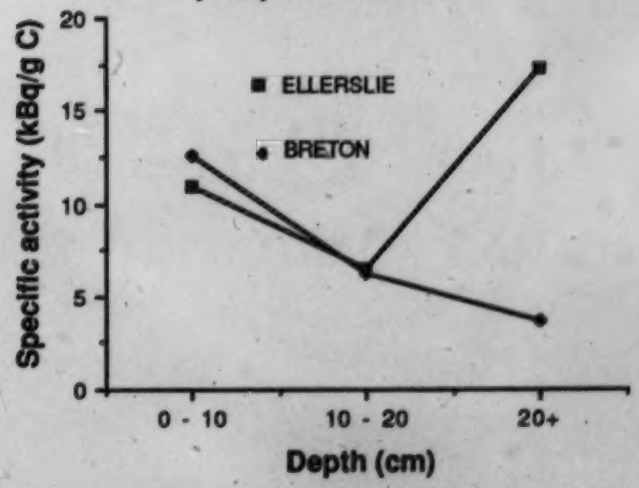
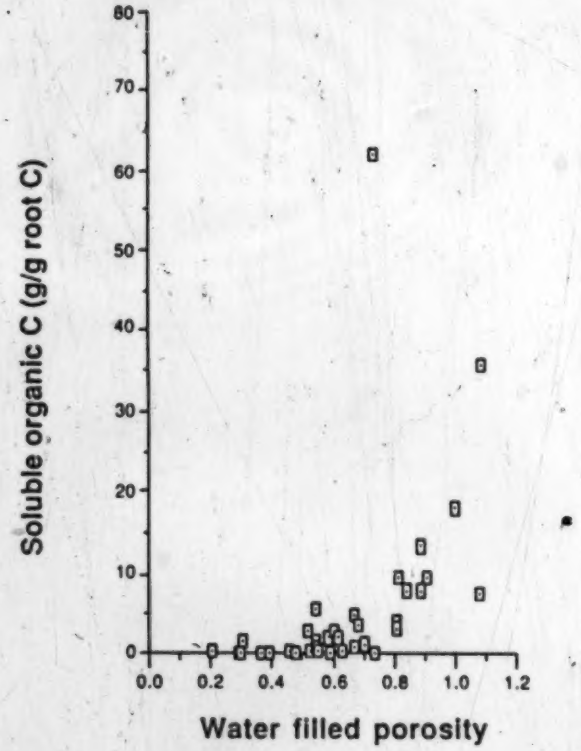



**Figure III.1. Site by day interaction for water filled porosity and site by depth interaction for unfumigated $CO_2$ specific activity at Ellerslie and Breton.**

2a. Effect of water filled porosity on soluble C (g/g root C)




2b. Analysis of water filled porosity effects on soluble C (g/g root C)

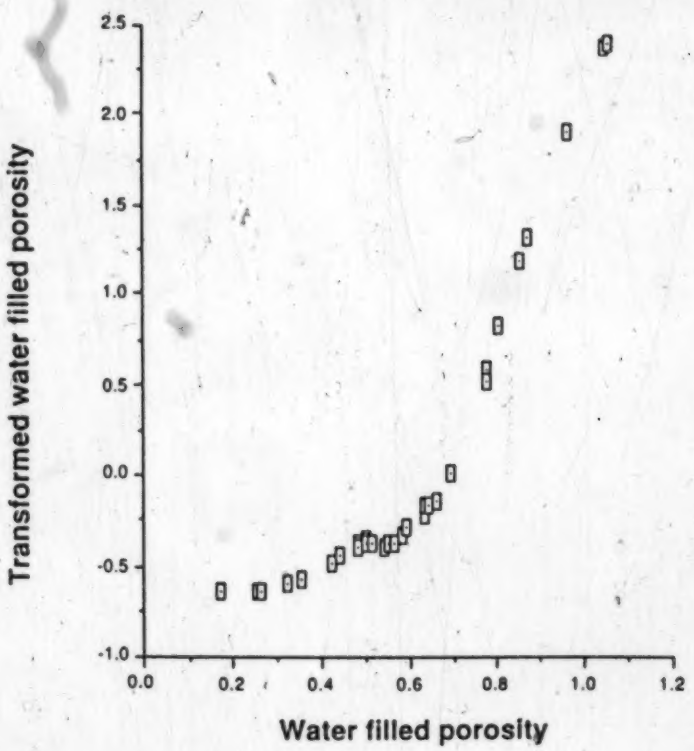



**Figure III.2. Effect of water filled porosity on soluble C (g/g root C).**

The amount of $^{14}C$ ($MBq/m^2$) in shoots > roots > microbial biomass at both sites (Table III.3). There were no differences between sites in the amount of $^{14}C$ found in any of these pools however soil $^{14}C$ was 12 to 76 times higher at Breton than Ellerslie ($p=0.0001$). None of the pools changed significantly over time. Root $^{14}C$ ($p=0.0081$), microbial $^{14}C$ ($p=0.0072$), and soil $^{14}C$ ($p=0.0537$) all decreased linearly with depth. Overall, the total recovery (%) of $^{14}C$ in the plant-soil system was 1.5 to 3.3 times higher at Breton than Ellerslie ($p=0.0924$), primarily because of the greater quantity of $^{14}C$ in the soil at Breton.

The specific activity (kBq/g C) of shoots > roots > microbial biomass (Tables III.4 and III.5). There were no differences between sites in the specific activity of any of the pools with the exception of soil $^{14}C$ which was 30 to 100 times higher at Breton than Ellerslie ($p=0.0023$). None of the pools changed significantly over time or with depth. The specific activity of $CO_2$ released from both fumigated and unfumigated soil samples during the 10-day laboratory incubations did not change over time (Table III.5). $CO_2$ released from unfumigated soil had a higher specific activity (0.6 - 28.9 kBq/g C) than $CO_2$ released from fumigated soil (0.5 - 10.8 kBq/g C) ($p=0.0543$). The specific activity of $CO_2$ from fumigated soil decreased linearly with depth ($p=0.0075$). The specific activity of $CO_2$ from unfumigated soil decreased with depth at Breton while at Ellerslie it decreased from the first to the second depth then increased in the 20+ cm depth (Fig. III.1(1b)). This resulted in an overall quadratic trend in the site by depth interaction ($p=0.0449$).

Because no significant changes over the four sampling dates were observed in the quantity of $^{14}C$ in the soil and microbial biomass or in the specific activity of respired $CO_2$, it was assumed that the soil system was in steady state with a constant influx of $^{14}C$ from labelled plant material. It was not possible to measure

Table III.3. $^{14}C$ budget ($MBq/m^2$) at Ellerslie and Breton.

| Compartment | Depth(cm) | Day of the year 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|---|
| | | | **Ellerslie** | | |
| **Shoot** | | 20.35 | 28.25 | 26.03 | 19.44 |
| **Root** | 0 - 10 | 0.42 | 0.45 | 0.49 | 0.51 |
| | 10 - 20 | 0.05 | 0.06 | 0.07 | 0.08 |
| | 20 + | 0.04 | 0.04 | 0.03 | 0.06 |
| **Microbial biomass** | 0 - 10 | 0.06 | 0.08 | 0.08 | 0.10 |
| | 10 - 20 | 0.01 | 0.04 | 0.02 | 0.02 |
| | 20 + | 0.01 | 0.004 | 0.004 | 0.002 |
| **Soil** | 0 - 10 | 0.42 | 2.29 | 0.59 | 0.60 |
| | 10 - 20 | 0.18 | 0.79 | 0.90 | 0.43 |
| | 20 + | 0.17 | 0.47 | 0.33 | 0.01 |
| **Total** | | 21.71 | 32.57 | 28.54 | 18.19 |
| **% Recovered** | | 18.59 | 27.85 | 24.43 | 18.18 |
| | | | **Breton** | | |
| **Shoot** | | 27.92 | 16.25 | 16.86 | 16.07 |
| **Root** | 0 - 10 | 1.61 | 1.21 | 1.09 | 1.59 |
| | 10 - 20 | 1.05 | 0.06 | 0.22 | 0.47 |
| | 20 + | 0.04 | 0.004 | 0.003 | 0.08 |
| **Microbial biomass** | 0 - 10 | 0.11 | 0.10 | 0.05 | 0.18 |
| | 10 - 20 | 0.08 | 0.04 | 0.01 | 0.04 |
| | 20 + | 0.03 | 0.003 | 0.01 | 0.00 |
| **Soil** | 0 - 10 | 11.56 | 12.39 | 9.61 | 11.33 |
| | 10 - 20 | 13.75 | 9.82 | 10.96 | 8.57 |
| | 20 + | 13.02 | 8.18 | 6.99 | 5.83 |
| **Total** | | 70.17 | 48.55 | 46.40 | 44.16 |
| **% Recovered** | | 60.82 | 42.05 | 39.91 | 38.58 |

**Summary of analysis of variance**

| Source of Variation | Shoot $^{14}C$ | Root $^{14}C$ | Microbial $^{14}C$ | Soil $^{14}C$ | Total $^{14}C$ |
|---|---|---|---|---|---|
| Site | ns | ns | ns | *** | $ |
| Date | ns | ns | ns | ns | ns |
| Site x Date | ns | ns | ns | ns | ns |
| Depth | | ** | ** | * | |
| Site x Depth | | ns | ns | ns | |
| Date x Depth | | ns | ns | ns | |
| Site x Date x Depth | | ns | ns | ns | |

$ - difference between the means significant at an adjusted $p<0.010$.

Table III.4. Specific activity (kBq/g C) at Ellerslie and Breton.

| Compartment | Depth(cm) | Day of the year 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|---|
| | | | **Ellerslie** | | |
| **Shoot** | | 149.2 | 150.7 | 76.8 | 84.9 |
| **Root** | 0 - 10 | 22.2 | 38.3 | 35.2 | 28.5 |
| | 10 - 20 | 18.3 | 28.9 | 23.8 | 21.9 |
| | 20 + | 31.0 | 31.0 | 24.6 | 27.5 |
| **Soil** | 0 - 10 | 0.09 | 0.45 | 0.11 | 0.13 |
| | 10 - 20 | 0.03 | 0.12 | 0.14 | 0.07 |
| | 20 + | 0.04 | 0.11 | 0.07 | 0.001 |
| | | | **Breton** | | |
| **Shoot** | | 224.8 | 101.0 | 98.9 | 165.6 |
| **Root** | 0 - 10 | 117.5 | 48.7 | 52.4 | 105.0 |
| | 10 - 20 | 375.2 | 39.5 | 61.7 | 235.9 |
| | 20 + | 121.5 | 8.1 | 15.9 | 278.2 |
| **Soil** | 0 - 10 | 4.8 | 5.6 | 4.1 | 5.1 |
| | 10 - 20 | 5.7 | 3.8 | 5.1 | 3.5 |
| | 20 + | 10.6 | 5.8 | 6.4 | 3.5 |

**Summary of analysis of variance**

| Source of Variation | Shoot | Root | Soil |
|---|---|---|---|
| Site | ns | ns | ** |
| Date | ns | ns | ns |
| Site x Date | ns | ns | ns |
| Depth | | ns | ns |
| Site x Depth | | ns | ns |
| Date x Depth | | ns | ns |
| Site x Date x Depth | | ns | ns |

the specific activity of the actual inputs but because the major output from the system was from microbial respiration, the specific activity of the $CO_2$ released during 10-day laboratory incubations was used to indicate the steady state specific activity of the active portion of the soil system. Active microbial C (%) was calculated from the following equation based on the assumption that the specific activity of the active microbial biomass was equal to that of the $CO_2$ released during 10-day laboratory incubations:

Table III.5 Specific activity (kBq/g C) of $CO_2$-C from fumigated and unfumigated incubations and of microbial biomass C at Ellerslie and Breton.

| Depth(cm) | Day of the year 212/223 | 230/244 | 251/265 | 272/293 |
|---|---|---|---|---|
| | **Fumigated** | | | |
| | **Ellerslie** | | | |
| 0 - 10 | 4.1 | 5.2 | 4.6 | 6.3 |
| 10 - 20 | 1.6 | 2.2 | 1.4 | 1.1 |
| 20 + | 2.3 | 1.9 | 1.3 | 0.9 |
| | **Breton** | | | |
| 0 - 10 | 10.3 | 6.6 | 6.4 | 10.8 |
| 10 - 20 | 5.7 | 1.9 | 2.3 | 3.7 |
| 20 + | 2.5 | 0.5 | 0.7 | 1.9 |
| | **Unfumigated** | | | |
| | **Ellerslie** | | | |
| 0 - 10 | 8.0 | 12.1 | 11.8 | 12.1 |
| 10 - 20 | 6.2 | 7.6 | 8.5 | 3.6 |
| 20 + | 28.9 | 13.6 | 22.0 | 4.8 |
| | **Breton** | | | |
| 0 - 10 | 14.9 | 8.8 | 12.7 | 14.0 |
| 10 - 20 | 11.4 | 1.8 | 4.5 | 7.3 |
| 20 + | 5.2 | 0.6 | 0.7 | 8.2 |
| | **Microbial C** | | | |
| | **Ellerslie** | | | |
| 0 - 10 | 1.4 | 2.0 | 1.6 | 2.4 |
| 10 - 20 | 0.2 | 0.7 | 0.4 | 0.5 |
| 20 + | 5.6 | 0.1 | 0.1 | 0.1 |
| | **Breton** | | | |
| 0 - 10 | 5.1 | 3.8 | 1.6 | 7.5 |
| 10 - 20 | 2.9 | 9.4 | 0.6 | 1.5 |
| 20 + | 2.3 | 0.7 | 0.7 | 0.0 |

**Summary of analysis of variance**

| Source of Variation | Fumigated C | Unfumigated C | Microbial C |
|---|---|---|---|
| Site | ns | ns | ns |
| Date | ns | ns | ns |
| Site x Date | ns | ns | ns |
| Depth | ** | * | ns |
| Site x Depth | ns | ** | ns |
| Date x Depth | ns | ns | ns |
| Site x Date x Depth | ns | ns | ns |

Table III.6. Active microbial C and carbon flow rate under laboratory conditions at Ellerslie and Breton.

| | Day of the year | | | |
|---|---|---|---|---|
| | 212/223 | 230/244 | 251/265 | 272/293 |
| | | | **Ellerslie** | |
| **Total microbial C ($g/m^2$)** | 112.1 | 113.3 | 120.2 | 118.4 |
| **Active microbial C (% of total)** | 14.6 | 11.9 | 17.1 | 25.1 |
| **Active microbial C ($g/m^2$)** | 16.4 | 13.5 | 20.6 | 29.7 |
| **Carbon flow rate ($g\ m^{-2}10d^{-1}$)** | 19.3 | 17.1 | 11.8 | 19.5 |
| | | | **Breton** | |
| **Total microbial C ($g/m^2$)** | 62.7 | 57.9 | 69.5 | 65.9 |
| **Active microbial C (% of total)** | 57.5 | 49.3 | 33.5 | 31.0 |
| **Active microbial C ($g/m^2$)** | 36.1 | 28.5 | 23.3 | 20.4 |
| **Carbon flow rate ($g\ m^{-2}10d^{-1}$)** | 21.9 | 31.4 | 22.5 | 21.2 |

**Summary of analysis of variance**

| Source of Variation | Active microbial C (%) | Active microbial C ($g/m^2$) | Flow rate |
|---|---|---|---|
| Site | * | ns | ** |
| Date | ns | ns | * |
| Site x Date | ns | ns | * |

$$\text{active microbial C (\%)} = \frac{\text{specific activity of measured microbial C}}{\text{specific activity of } CO_2} \times 100$$

Active microbial C (%) at Breton was approximately 2 times higher than at Ellerslie ($p=0.0181$) (Table III.6). Differences between sites in the quantity of active microbial C were not significant because the total microbial C was approximately 2 times higher at Ellerslie than at Breton ($p=0.0020$) (Table III.6). Flow rates of carbon (Table III.6) were calculated from the sum of the quantity of $CO_2$-C respired from all three depths during unfumigated 10-day laboratory incubations. The respiration of $CO_2$-C during 10-day laboratory incubations has been described above in more detail (Table III.1).

## Discussion

### Distribution of $^{14}C$ after labelling

The distribution of $^{14}C$ after pulse labelling depends on environmental conditions at, and shortly after, the time of labelling. Carbon fixation and allocation in plants is affected by light, temperature, $CO_2$ (Enoch and Hurd 1977), moisture (Biscoe et al. 1975) and nutrient availability (Powell and Ryle 1978) all of which can vary in time and/or space when labelling is done in the field. When the fate of $^{14}C$ after pulse labelling is followed over time, fluctuations in the measured activity between sampling dates may be due to spatial variability in the uptake and allocation of $^{14}C$ and in the subsequent growth of the plants (Dahlman and Kucera 1967). Despite these drawbacks, pulse labelling techniques remain the most practical for field studies (Røsberg et al. 1981).

The activities of the shoot, root, and microbial pools were similar between sites but approximately 50 times more $^{14}C$ remained in the soil organic matter at Breton than Ellerslie on the first sampling date. Since the $^{12}C$ budget showed that the Gray Luvisol at Breton was lower in organic matter than the Black soil at Ellerslie (Table II.2), the increased retention of $^{14}C$ may be due to temporary differences in conditions at the time of labelling. Although the two sites were labelled on different days, environmental conditions were the similar with the exception of higher soil moisture at Breton.

The influence of soil moisture on carbon retention can be determined by examining the relationship between soluble C and water filled porosity. Soluble C (g/g root C), which is an estimate of the quantity of root derived C in the soil, increased when water filled porosity was greater than 70% (Fig. III.2). Soluble C forms the main source of carbon and energy for rhizosphere bacteria (Newman 1985) therefore, when $O_2$ is available, much of the soluble C is lost as $CO_2$ due to microbial respiration. Under anaerobic conditions fermentation replaces respiration

as the main catabolic process in roots (Wiedenroth 1981) and this may lead to an increase in the quantity of soluble C in soil. Linn and Doran (1984) have found that above 60% water filled porosity anaerobic processes in soil begin to replace aerobic processes and the release of $CO_2$ from soil decreases. Toxic products in roots accumulate during fermentation and must be exuded from the roots (Wiedenroth 1981). Anaerobic conditions increase root porosity (Benjamin and Greenway 1979) which could promote loss of soluble carbon from roots. Roots which are mechanically impeded by high bulk density, as they were at Breton (Table II.1), are more sensitive to $O_2$ concentration than are unimpeded roots (Schumacher and Smucker 1981). Wiedenroth and Poskuta (1981) observed an increase in the quantity of root derived carbon in rooting media under anaerobic conditions. They attributed it to increased loss of root C however their system was not sterile so that it is not possible to rule out the effects of decreased microbial respiration. High water filled porosity at Breton at the time of labelling may have caused increased retention of $^{14}C$ in the soil due to increased loss of C from roots and/or decreased microbial respiration.

**Dynamics of $^{14}C$ after labelling**

Even though the plants were pulse labelled, the constant quantity of $^{14}C$ in the soil pools and the constant specific activity of the respired $CO_2$ indicated that the soil system was behaving as if in steady state with a constant influx of $^{14}C$ from labelled plant material. Release of $^{14}C$ to soil after pulse labelling is controlled by allocation of carbon to the various types of compounds formed by the plant. Labelled carbon enters the soluble pool first and turns over quickly as that carbon which is not lost by respiration is allocated to storage and structural pools (Gordon et al. 1977) which have lower turnover rates (Prosser and Farrar 1981). Milchunas et al. (1985) found that after pulse labelling wheat the allocation of $^{14}C$ to shoot, root, and soil organic matter was essentially complete after 5 days. $^{14}C$ in soil was

the highest at 3.5 hr after labelling and then declined after 5 days to a level which remained constant for the remaining 62 days. After pulse labelling living plants, an initial pulse of $^{14}C$ appears as soluble root exudates followed by a more constant release of $^{14}C$ caused by the turnover of labelled storage and structural material. The soil system may reach steady state conditions with the input of labelled carbon from storage and structural root tissue.

When a system is receiving a constant level of tracer input and has reached steady state, each pool in the system should have the same specific activity as the input and output from the system if the label is uniformly mixed throughout each pool (Shipley and Clark, 1972). Even though the soil system in this study appeared to be in steady state the specific activity of the microbial biomass was less than the specific activity of respired carbon. This would occur if the $^{14}C$ was not uniformly mixed in the microbial biomass pool because part of the measured pool was not actively turning over, as proposed by Hunt (1977) and van Veen et al. (1984). The difference between the specific activity of the microbial biomass and that of respired C indicated that on average 43% of the measured microbial biomass was active at Breton while 17% was active at Ellerslie. These values fall within the range reported by others in the literature. For example, Clarholm and Rosswall (1980) estimated that 15 to 30% of the biomass was active in a forest soil and a peat. Merckx et al. (1986), using a continuous labelling procedure, found that only 5.6% of the biomass was active at the end of the experiment. Helal and Sauerbeck (1986), using the same technique, found that an average of 45% of the microbial biomass was active after 30 days.

Since the system at both sites behaved as if it was at steady state with respect to $^{14}C$, the specific activity of the soil pool should also be the same as the specific activity of carbon respired from the system. At Ellerslie the specific activity of the soil organic pool was less than that of the respired carbon indicating that

some of the total organic carbon was not turning over at the same rate as $^{14}C$ released from root material. At Breton, however, the specific activity of the soil organic carbon was higher than at Ellerslie and at times higher than the specific activity of respired carbon. The quantity of $^{14}C$ in the soil at Breton was higher than at Ellerslie. This may be due to conditions of high water filled porosity at the time of labelling.

$O_2$ concentration in soil affects the proportion of added carbon which remains as organic matter. Low $O_2$ concentrations (5%) are optimum for organic matter formation from complex substrates such as straw while higher $O_2$ concentrations (20%) are optimum for simple compunds such as glucose (Novak 1983). The composition of root exudates changes under anaerobic conditions as energy rich, low molecular weight products of fermentation are released (Wiedenroth 1981). Novak (1983) found that more carbon from decomposing plant residue was stabilized in soil when aerobic incubation was preceded by a 10-day anaerobic pretreatment, than under aerobic or anaerobic incubation alone. In our study soil moisture conditions at the time of labelling may have changed the composition of root exuded carbon. A subsequent increase in soil aeration may have enhanced the stabilization of these compounds in soil organic matter.

Anaerobic conditions also increase the quantity of root exuded carbon and decrease respiratory activity as discussed above. Using an artificial root system, Martens (1982) observed that if microbial biomass could not use all of the glucose released, some of the excess carbon formed insoluble polysaccharide around the root while some diffused away from the root. The mechanism by which the polysaccharide formed was not known. If the microbial biomass in our study had been unable to use of all of the additional carbon released under anaerobic conditions, the formation of insoluble compounds may have enhanced the stabilization of root derived carbon.

If some of the $^{14}C$ was no longer actively turning over a turnover rate for the system as a whole cannot be calculated since accurate pool sizes cannot be determined. It is possible, however, to compare the flow rate out of the systems at Ellerslie and Breton from the quantity of $CO_2$ ($g/m^2$) respired during 10-day laboratory incubations since respiration represents the major loss of carbon from the system. Carbon flow rates out of the system at Breton were up to 2 times higher than Ellerslie. This difference between sites does not seem to have been due to soil moisture even though water filled porosity was higher at Breton than Ellerslie. Carbon flow rates were calculated from the quantity of $CO_2$-C respired during 10-day incubation under constant moisture conditions. Differences in soil moisture at the time of sampling did not seem to affect C flow rates because the changes in carbon flow rates over time did not follow the same pattern as changes in water filled porosity.

Soil characteristics and cropping history may also have an effect on the cycling of carbon through the soil system. Van Veen et al. (1984) proposed that different soils have different microbial biomass preservation capacities. Juma et al. (1984) found that after the addition of $^{14}C$-glucose more $^{14}CO_2$ was released from a Gray Luvisol than a Black soil under constant moisture conditions. Merckx et al. (1985) observed that the turnover of root derived carbon was faster and more constant in a sandy soil than a clay soil. This is consistent with the textural differences between the soils at Breton (L) and Ellerslie (SiCL). McGill et al. (1986) have observed that crop rotations influence carbon turnover, with faster microbial and soluble carbon turnover in a wheat-fallow rotation than a 5-year rotation with 2 years of forages. The plot area at Ellerslie had been in bromegrass-alfalfa for 14 years before being cropped to barley in 1985 while Breton had been in barley or fallow during the same period. Both pedogenic soil characteristics and cropping histories may have influenced the differences in carbon flow rate and

percentage of active microbial biomass between the two sites. These differences in C cycling will affect the fate of carbon residues added to the soil and thus have important implications for agronomic practices and the maintenance of organic matter levels in soil.

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## Chapter 4. Synthesis

### Summary

In the course of this study a general picture has emerged of carbon cycling in a Gray Luvisol and a Black soil cropped to barley. There was less $^{12}C$ in the system at Breton than at Ellerslie and all carbon pools with the exception of root C were smaller at Breton. The distribution of carbon, as measured by $^{14}C$ pulse labelling, differed from the cumulative distribution of carbon over time, as integrated in $^{12}C$ measurements. The effect of short term changes in environmental conditions was observed in the $^{14}C$ pulse labelled study but not in the long term accumulation of $^{12}C$.

Both $^{12}C$ and $^{14}C$ techniques provided information on the relationship between carbon distribution and dynamics at both sites. The distribution of soil C between different kinetic pools indicated that a larger proportion of soil C was in the less stable microbial and soluble pools at Breton than Ellerslie. In addition to this, a larger proportion of the microbial biomass was active at Breton than Ellerslie leading to respiration rates which were higher in proportion to the total quantity of microbial C at Breton. Potential flow rates of carbon out of the soil ($g/m^2$), determined in laboratory incubations, were greater at Breton than Ellerslie. Again, the $^{14}C$ data indicated that short term fluctuations in environmental conditions caused changes in carbon dynamics which were not noticeable in long term carbon accumulation. Moisture conditions at the time of labelling caused greater stabilization of exuded $^{14}C$ at Breton than at Ellerslie even though subsequent measurements on the four sampling dates indicated that soil C was less stable and microbial use less efficient at Breton.

### $^{12}C$ versus $^{14}C$ data

While the use of both $^{12}C$ and $^{14}C$ measurements can give complementary information, it is important to note that $^{12}C$ is accumulated over a much long time

period than $^{14}C$, when $^{14}C$ is applied with pulse labelling techniques. The controlling factors operating at different time scales are not the same (Meentemeyer and Box 1987) and caution is required when comparing information derived from the two methods. Plants control carbon input to agroecosystems. The biological processes which influence above and belowground carbon pool sizes in the plant are photosynthesis, which governs carbon uptake; respiration and root exudation, which govern losses of carbon from the plant; and the pattern of carbon allocation within the plant. Each of these processes is controlled by several factors.

Photosynthesis is affected by environmental factors such as temperature, $CO_2$ levels, and light (Enoch and Hurd 1977); moisture (Biscoe et al. 1975b), nitrogen supply (Powell and Ryle 1978), and stage of plant growth (Ryle 1972).

Respiration is influenced by temperature (Farrar 1980) and stage of plant growth (Biscoe et al. 1975b). The ratio of respiration/photosynthesis, which governs how much of the fixed carbon remains in the plant, is also affected by growth stage (Winzeler et al. 1976). Respiration/assimilation is dependant on the time of day at which the carbon is incorporated (Morgan and Austin 1983).

The loss of carbon from roots is affected by a number of factors including stage of plant growth (Martin, 1975a), pH (McDougall, 1970), bulk density (Barber and Gunn, 1974; Schwonwitz and Zeigler, 1982), $pO_2$ in the root environment (Wiedenroth and Poskuta, 1981), soil moisture potential (Martin, 1977b), plant nutrient status (Trolldenier, 1975), temperature (Martin, 1977a), and photoperiod (Whipps, 1984).

The pattern of carbon allocation within the plant at a given time is affected by the stage of plant growth (Martin and Kemp 1986) as well as a number of environmental factors such as light intensity and nitrogen availability (Powell and Ryle 1978), the difference between root and shoot temperatures (Davidson 1969), and $pO_2$ in the soil (Trought and Drew 1980).

The quantity of $^{12}C$ in a given pool represents an integration over time of changes in carbon allocation caused by changes in these processes. The time period over which this integration occurs is not the same for all parts of the plant-soil system. Shoots and roots in an annual cropping system integrate changes in carbon allocation caused by ontogeny and changing weather conditions (Biscoe et al. 1975a). The quantity of organic carbon in soil will depend on longer term pedogenic factors such as soil texture and vegetation as well as shorter term agronomic practices (Campbell and Souster 1982).

The quantity $^{14}C$ found in the various components of the plant-soil system after pulse labelling provides a description of carbon allocation at a specific growth stage and under a specific set of environmental conditions. Because factors controlling these processes show considerable temporal variation, care must be taken in the extrapolation of this type of data to other points in time (Røsberg et al. 1981). The use of $^{12}C$ and $^{14}C$ data together will give information on both long term accumulations of carbon and the way in which temporary changes in environmental conditions affect carbon allocation.

**$^{14}C$ versus $^{12}C$ distribution**

In spite of the large number of factors which can affect a pulse labelling experiment, it remains the most practical for $^{14}C$ tracer studies in the field (Whipps and Lynch 1983). A number of studies using both pulse and continuous labelling techniques have been carried out in the field and in growth chambers. When the results are compared from those experiments in which the type of plant and stage of growth were most similar to this study, the continous labelling experiments show a greater amount of belowground translocation than do the pulse labelled experiments (Table IV.1). There are two probable reasons for this. Firstly, a continous labelling technique integrates carbon allocation over the life of the plant. Keith et al. (1986),

Table IV.1. $^{14}C$ distribution in cereal plants.

| Site* | Plant§ | Age (days) | S/R† | % $^{14}C$ recovered in Shoot | Root | Soil | Micr. C. | Root/Soil Resp. | References |
|---|---|---|---|---|---|---|---|---|---|
| | | | | **Pulse Labelled** | | | | | |
| F | B | 55 | 11.5 | 93.8 | 2.3 | 3.5 | 0.4 | na | Chapter 2, Ellerslie |
| F | B | 65 | 7.3 | 40.0 | 3.8 | 56.0 | 0.3 | na | Chapter 2, Breton |
| F | W | 98 | na | 89.1 | 1.5 | 5.3 | na | 4.1 | Keith et al. 1986 |
| F | W | 70 | na | 90.5 | 5.2 | | na | 4.3 | Martin & Kemp 1986 |
| GC | W | 45 | 0.9 | 49.3 | 42.7 | 8.0 | na | na | Milchunas et al. 1985 |
| GC | W | 60 | 2.0 | 67 | 10 | na | na | 23 | Warembourg & Paul 1973 |
| | | | | **Continuously Labelled** | | | | | |
| GC | M | 30 | na | 57.0 | 24.0 | 1.1 | 1.6 | 16.3 | Helal & Sauerbeck 1986 |
| GC | W | 42 | 1.1 | 49.6 | 29.7 | 1.0 | 0.2 | 19.5 | Merckx et al. 1985 |
| GC | W | 42 | 0.7 | 60 | 25 | 3 | 1 | 11 | Merckx et al. 1985 |
| GC | M | 42 | 1.3 | 70.6 | 27.8 | 1.5 | na | na | Merckx et al. 1986 |
| GC | W | 42 | 1.1 | 61.3 | 36.7 | 2.0 | na | na | Merckx et al. 1986 |

na - not available
† - Shoot/root ratio
* - F-field, GC-growth chamber
§ - B-barley, W-wheat, M-maize

using a pulse labelling technique, have shown that belowground translocation in wheat decreases as plants mature. $^{14}C$ distribution in continuously labelled plants is affected by higher rates of belowground translocation at early growth stages while $^{14}C$ distribution in plants which are pulse labelled at later growth stages show only the carbon allocation pattern for that point in time. Secondly, the difference in shoot/root ratios between growth chamber and field studies has probably influenced the allocation of $^{14}C$ as well. Shoot/root ratios are higher in plants grown in the field than in those grown in growth chambers as can be seen from our field data and the data of those experiments carried out in growth chambers (Table IV.1). Our shoot /root ratios fall within the same range found by Welbank et al. (1973) and Biscoe et al. (1975b) for barley in England and by Brown et al. (1987) for barley in Syria.

The allocation of $^{14}C$ within the plant-soil system at Ellerslie was similar to that found by other researchers. However, an unusually large quantity of $^{14}C$ was found in the soil at Breton. Apparently temporary differences in environmental conditions caused the difference in $^{14}C$ distribution. As stated in Chapter 3, the primary factor influencing this difference was probably the difference in water filled porosity between sites at the time of labelling. The behaviour of soluble carbon with respect to water filled porosity supports this finding. Soluble C (g/g root C), a measure of root derived C, began to increase at water filled porosities above 70%. This is in the same range of water filled porosity at which Linn and Doran (1984) found anaerobic soil processes replace aerobic. Wiedenroth and Poskuta (1981) have shown that 4 to 6 times more of the carbon translocated from shoots to roots is found in anaerobic rooting media than in well aerated media. When carrying out pulse labelling experiments differences in environmental conditions will cause differences in carbon allocation that may make a comparison of different sites or labelling times difficult.

In general shoot and root $^{12}C$ yields were lower than those published in the literature. Most reports of shoot and root yields are reported in units of dry matter therefore a carbon content of 40% has been assumed for purposes of comparison. Shoot C was up to 3 times lower at Ellerslie and 2 to 4 times lower at Breton than was found by Welbank et al. (1973) and Biscoe et al. (1975b) for barley in England and by Brown et al. (1987) for barley in Syria. Root C yields at both sites were up to 3 times lower. The distribution of roots with depth at both sites was similar to that found by Welbank et al. (1973).

The concentration of organic C found at Breton was about 1.5 times higher than that found by McGill et al. (1986) but similar to that found by Reinl (1984) in a number of Gray Luvisols in Alberta. The organic C concentration at Ellerslie was intermediate between that found by Reinl (1984) for cultivated and virgin Black

soils. This may be because Ellerslie was in bromegrass-alfalfa for 14 years prior to the study.

The quantity of microbial C in soil tends to reflect the amount of soil organic matter (Jenkinson and Ladd, 1981). Seasonal variations in environmental conditions, especially moisture and temperature, cause fluctuations in the overall quantity of microbial C (Campbell and Beiderbeck 1976, McGill et al. 1986). The quantity of microbial C also increases as root mass increases during the growing season (Darbyshire and Greaves 1967, Lynch and Panting 1980). This is related to plant growth stage with microbial biomass increasing until plant reproductive stages and then decreasing (Carter and Rennie 1984). The quantity of microbial biomass C at Breton was in the same range as that reported by McGill et al. (1986) in a wheat-fallow rotation at Breton (26-32 mg/100 g soil, 0-5 cm depth). Microbial C at Ellerslie was approximately 1.5 times less than that found in a conventionally tilled Black soil by Carter and Rennie (1982).

The quantity of soluble C in soil can fluctuate markedly over time (Dormaar et al. 1984) and space (Foloronso and Rolston 1985). Dormaar et al. (1984) found that the quantity of soluble C was less in a low organic matter Brown soil than in a higher organic matter Black soil. This study found the same pattern with less soluble C in the low organic matter Gray Luvisol at Breton than in the high organic matter Black soil at Ellerslie. In general the quantity of soluble C found was in the same range as that found by McGill et al. (1986) and Foloronso and Rolston (1985) but 2 to 3 times less than that found by Dormaar et al. (1984).

The concentration of polysaccharide C in soil tends to be closely tied to the quantity of soil organic matter (Lowe 1978). The quantity of polysaccharide C at Breton was similar to that found at Breton by Sawyer and Pawluk (1963). Polysaccharide C concentrations at Ellerslie were more than those found in other Black soils by Graveland and Lynch (1961) (2.0-3.5 mg/g soil) and Acton et al.

(1963) (3.5-5mg/g soil). The polysaccharide concentrations found in this study may be higher than those of Graveland and Lynch (1961) and Acton et al. (1963) due to a more vigorous hydrolysis procedure.

**$^{12}C$ and $^{14}C$ dynamics**

Information about carbon dynamics can be obtained from both $^{12}C$ and $^{14}C$ data. Changes in biomass have been used to estimate aboveground (Dickerman et al. 1986) and belowground (Hanson and Steen 1985) plant production and microbial biomass dynamics (McGill et al. 1986). The use of such data requires more sampling dates than were available in this study (Dickerman et al. 1986). Alternatively, some inferences about carbon dynamics can be made by determining the relative proportion of carbon located in various kinetic pools in the system. This approach was taken with the $^{12}C$ data in Chapter 2. $^{14}C$ tracer techniques can be used to determine carbon dynamics more directly and accurately by measuring the loss of activity after pulse labelling or the equilibrium specific activity of a pool in a continuously labelled system.

As discussed in Chapter 2, soluble and microbial C formed a larger proportion of the soil C in the low organic matter Gray Luvisol at Breton than in the high organic matter Black soil at Ellerslie. Dormaar et al. (1984) found that soluble C made up a larger proportion of soil organic C in a low organic matter Brown soil than a high organic matter Black soil. Both soluble C and microbial C are more active than soil organic C as a whole thus carbon in the soil at Breton appears to be less stable than at Ellerslie. Although soluble C and microbial C as fractions of soil organic C showed differences between sites, polysaccharide C did not. This is consistent with reports in the literature. Oades (1967) found that while the quantity of polysaccharide C changes as organic matter levels change with different soils and crop rotations, the proportion of polysaccharide C in soil organic matter remains

constant. Polysaccharide forms a constant 6-14% of soil organic C (Lowe 1978). The values found in this study fall within this range as well.

Differences in soil C stability between sites were accompanied by differences in microbial activity. $^{14}C$ data was used to calculate the proportion of active microbial C at Ellerslie and Breton. On average 17% of the microbial biomass was active at Ellerslie while 43% was active at Breton. These values are similar to those of Clarholm and Rosswall (1980) and Helal and Sauerbeck (1986). However Merckx et al. (1986), using a continuous labelling technique similar to that of Helal and Sauerbeck (1986), estimated that only 5.6% of the biomass was active.

Differences in the proportion of active microbial C were associated with a greater release of $CO_2$ from the microbial biomass (g $CO_2$-C/g microbial C) and a greater flow of carbon out of the system (g $CO_2$-C/$m^2$) at Breton than at Ellerslie. Similar results were obtained by Juma et al. (1984) who found that more $^{14}C$ was respired from a Gray Luvisol than a Black soil after the addition of $^{14}C$-glucose. The mineralization of carbon is closely tied to nitrogen mineralization (Stewart et al. 1982). Campbell and Souster (1982) found that potentially mineralizable nitrogen made up a larger fraction of total nitrogen in Gray Luvisols than in Black soils.

The specific activity of soil C at Ellerslie showed that much of the carbon in the soil was not turning over as fast as the labelled fraction. Merckx et al. (1985) obtained similiar results in their continuously labelled experiments. In their study, the specific activity of the soil at equilibrium was approximately 100 fold less than the specific activity of the plant material.

**Factors affecting C cycling**

When comparing these differences in carbon cycling between Gray Luvisols and Black soils, it is difficult to separate out the complicating factors of differences in soil texture and cropping history. Both may influence the aspects of carbon

cycling measured in this study. Campbell and Souster (1982) found that potentially mineralizable nitrogen as a fraction of total nitrogen increased as soil texture became more coarse. Merckx et al. (1985) found more belowground $CO_2$ was released from a sandy soil planted to wheat than from a silt loam. Cropping history may have influenced carbon turnover at the two sites although its influence on carbon allocation is less clear. The Ellerslie site was in bromegrass-alfalfa from 1971-1985 while the Breton site was in barley or fallow. Microbial biomass turnover (McGill et al. 1986) and turnover of soluble amino acids (Monreal 1987) are faster in a wheat-fallow rotation than in a 5-year rotation. Campbell and Souster (1982) found that potentially mineralizable nitrogen formed a larger proportion of total nitrogen in virgin than cultivated Black soils while, in general, this trend was reversed in Gray Luvisols. Voroney et al. (1981) found that microbial biomass formed a smaller proportion of soil organic matter in a virgin than in a cultivated Black soil. Biederbeck et al. (1984) found no difference in potentially mineralizable nitrogen as a percentage of total nitrogen between different crop rotations.

Nitrogen availability may have also affected the allocation of carbon within the soil at Breton. As mentioned in Chapter 2, the plants at Breton were nitrogen deficient while those at Ellerslie were not. This was probably due to the loss of nitrogen at Breton caused by saturated soil conditions in July. Biederbeck et al. (1984) found that microbial biomass made up a larger percentage of soil organic C in a nitrogen deficient crop rotation than in soil which received adequate nitrogen.

## Conclusions

The use of $^{12}C$ and $^{14}C$ data has given complementary information about carbon cycling at Ellerslie and Breton. Allocation of C within the plant-soil system as determined by a $^{12}C$ budget is different from that determined by $^{14}C$ due to the time scales involved. Fluctuations in environmental conditions which affect the allocation of carbon temporarily are revealed by pulse labelling techniques. In this

study, high water filled porosity at the time of labelling increased the quantity of $^{14}C$-labelled root material in the soil at Breton. Because the $^{12}C$ data integrated such changes over the growing season it revealed a more general pattern of carbon distribution.

Overall, $^{12}C$ pool sizes were lower at Breton than Ellerslie. This is consistent with the findings of other researchers. $^{12}C$ data showed that a larger proportion of soil C was located in the less stable soluble and microbial C pools at Breton than at Ellerslie, that microbial use of carbon was less efficient at Breton, and that the flow rate of carbon out of the soil was greater at Breton than Ellerslie. $^{14}C$ data revealed that a larger fraction of the microbial biomass was active at Breton than at Ellerslie. Overall the soil system at Breton seemed to be less stable and the microbial biomass more active than at Ellerslie.

**Implications for soil management**

This study has found differences in the amount of carbon stabilized and in the quantity of C respired between sites. Since carbon cycling is tied to crop production either directly or indirectly through its effect on soil structure, water holding capacity, and fertility (Johnston 1982, Hedlin 1986), the maintainence of organic matter levels is an important goal in agricultural management. If more carbon is respired and less is stabilized at Breton, then more care must be taken in attempting to maintain organic matter levels. A knowledge of the influence of crop management on carbon cycling is important in crop management. If a given area is susceptible to organic matter loss, either because of soil order or other soil characteristics such as soil texture, then appropriate crop rotations must be developed which increase carbon stability and maintain crop production. An understanding of carbon cycling in different soil orders and factors affecting the process such as soil texture, cropping history, and environmental conditions will

allow a more site specific adjustment of agronomic practices for optimum production.

**Future research**

A number of questions remain to be answered:

1. What is the effect of soil order, soil texture, and agronomic management in carbon cycing and the stabilization of organic C in soil?

   This study has been unable to separate the influences of these three but as indicated above all three may play a role in C cycling.

2. Does the rate of carbon turnover in the rhizosphere affect crop yield?

   McGill et al. (1986) have found carbon turnover was slower and crop yield higher in a 5-year rotation than a 2-year wheat-fallow rotation. Microbial activity increases the quantity of carbon exuded from roots (Martin 1975a) and this competition for photosynthate may reduce plant growth (Ryle et al. 1979).

3. How do Black soils and Gray Luvisols respond to differences in cropping practices?

   Different soils do not respond in the same way to similar conditions. Martin (1987) found that less soil organic matter was mineralized in a soil in which plants were growing than from unplanted soil while Helal and Sauerbeck (1986), working with a different soil, found the opposite. Gray Luvisols may respond differently to cultivation than Black soils. Potentially mineralizable nitrogen makes up a smaller proportion of total nitrogen in virgin Gray Luvisols than in virgin Black soils while this trend is reversed after cultivation (Campbell and Souster 1982). Thus a given crop rotation may not have the same affect on carbon and nutrient cycling in the two different soils.

A careful selection of study sites to minimize the number of variables affecting carbon cycling and a combination of $^{12}C$ and $^{14}C$ techniques may be needed to gain the required information. Field studies pose problems due to uncontrollable environmental variation, particularly for pulse labelled $^{14}C$ studies. Despite this fact, it may not be possible to study the long term interactions between

crop rotations and soil properties under any other conditions. Learning to deal with environmental variation may be a better approach to this type of study than the attempt to remove variation by using growth chambers. A great deal of information regarding the interactions between soil, crops, and the sequence of cropping practices will be gathered as we begin to apply techniques and gather data suitable to long term studies.

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# Appendices

## Appendix 1. Additional data.

Table A1.1. Gravimetric moisture content and bulk density at Ellerslie and Breton

| | Day of the year§ | | | |
|---|---|---|---|---|
| Depth (cm) | 212/223 | 230/244 | 251/265 | 272/293 |
| | Gravimetric moisture content (Mg/Mg) | | | |
| | | Ellerslie | | |
| 0 - 10 | 0.337 | 0.159 | 0.129 | 0.387 |
| 10 - 20 | 0.292 | 0.199 | 0.169 | 0.363 |
| 20 + | 0.292 | 0.202 | 0.201 | 0.349 |
| | | Breton | | |
| 0 - 10 | 0.261 | 0.140 | 0.289 | 0.309 |
| 10 - 20 | 0.235 | 0.201 | 0.209 | 0.260 |
| 20 + | 0.229 | 0.217 | 0.217 | 0.244 |
| | Bulk density ($Mg/m^3$) | | | |
| | | Ellerslie | | |
| 0 - 10 | 0.877 | 0.803 | 0.897 | 0.843 |
| 10 - 20 | 1.096 | 1.094 | 1.054 | 1.005 |
| 20 + | 1.087 | 1.130 | 1.233 | 1.191 |
| | | Breton | | |
| 0 - 10 | 1.099 | 1.165 | 1.061 | 1.064 |
| 10 - 20 | 1.285 | 1.265 | 1.338 | 1.312 |
| 20 + | 1.561 | 1.580 | 1.615 | 1.442 |

**Summary of analysis of variance**

| Source of Variation | Moisture | Bulk density |
|---|---|---|
| Site | ns | *** |
| Date | *** | ns |
| Site x Date | * | ns |
| Depth | ** | *** |
| Site x Depth | ns | $ |
| Date x Depth | * | ns |
| Site x Date x Depth | ns | ns |

§ - sampling date for Ellerslie and Breton respectively

The difference between means is significant at: ns, not significant; *, adjusted $p<0.05$; **, adjusted $p<0.01$; ***, adjusted $p<0.001$.

Table A1.2. Shoot and root mass ($g/m^2$) at Ellerslie and Breton.

| | | Day of the year§ | | | |
|---|---|---|---|---|---|
| Compartment | Depth(cm) | 212/223 | 230/244 | 251/265 | 272/293 |
| | | | **Ellerslie** | | |
| **Shoot** | | 540.7 | 1561.7 | 878.2 | 650.0 |
| **Root** | 0 - 10 | 110.7 | 40.8 | 45.4 | 62.1 |
| | 10 - 20 | 17.0 | 10.5 | 17.3 | 12.5 |
| | 20 + | 7.5 | 5.0 | 6.9 | 7.8 |
| | | | **Breton** | | |
| **Shoot** | | 582.4 | 450.3 | 419.6 | 278.7 |
| **Root** | 0 - 10 | 64.8 | 72.4 | 61.9 | 53.8 |
| | 10 - 20 | 8.8 | 5.1 | 6.3 | 6.6 |
| | 20 + | 1.2 | 1.5 | 0.6 | 1.0 |

**Summary of analysis of variance**

| Source of Variation | Shoot | Root |
|---|---|---|
| Site | $ | ns |
| Date | ns | ns |
| Site x Date | $ | ns |
| Depth | | *** |
| Site x Depth | | $ |
| Date x Depth | | ns |
| Site x Date x Depth | | ns |

§ - sampling date for Ellerslie and Breton respectively

The difference between means is significant at: ns, not significant; $, adjusted $p<0.010$; *, adjusted $p<0.05$; **, adjusted $p<0.01$; ***, adjusted $p<0.001$.

Table A1.3. Shoot, root, and soil carbon concentration (%) at Ellerslie and Breton.

| | | Day of the year§ | | | |
|---|---|---|---|---|---|
| Compartment | Depth(cm) | 212/223 | 230/244 | 251/265 | 272/293 |
| | | | **Ellerslie** | | |
| **Shoot** | | 37.35 | 41.90 | 41.60 | 41.08 |
| **Root** | 0 - 10 | 18.15 | 30.50 | 29.92 | 31.8 |
| **Soil** | 0 - 10 | 6.42 | 6.41 | 6.43 | 6.60 |
| | 10 - 20 | 6.48 | 6.14 | 6.28 | 6.39 |
| | 20 + | 5.34 | 5.31 | 4.97 | 5.30 |
| | | | **Breton** | | |
| **Shoot** | | 26.87 | 36.19 | 38.00 | 34.08 |
| **Root** | 0 - 10 | 26.12 | 30.87 | 28.98 | 29.50 |
| **Soil** | 0 - 10 | 2.20 | 2.01 | 2.28 | 1.18 |
| | 10 - 20 | 1.94 | 2.18 | 1.67 | 1.89 |
| | 20 + | 1.04 | 1.30 | 1.00 | 1.17 |

**Summary of analysis of variance**

| Source of Variation | Shoot | Root | Soil |
|---|---|---|---|
| Site | * | ns | *** |
| Date | ** | ** | ns |
| Site x Date | ns | ns | ns |
| Depth | | | ** |
| Site x Depth | | | ns |
| Date x Depth | | | ns |
| Site x Date x Depth | | | ns |

§ - sampling date for Ellerslie and Breton respectively

The difference between means is significant at: ns, not significant; *, adjusted $p<0.05$; **, adjusted $p<0.01$; ***, adjusted $p<0.001$.

## Appendix 2. Example of statistical analysis.

Table A2.1. Analysis of variance of water-filled porosity.

| Source | d f | SS | F | Pr>F | eps. | adj. d f | adj. Pr>F |
|---|---|---|---|---|---|---|---|
| Site | 1 | 0.70 | 25.87 | 0.0070 | | | |
| Error: Reps/Site | 4 | 0.11 | | | | | |
| Date | 3 | 0.48 | 12.69 | 0.0005 | 0.60 | 1.8 | 0.0049 |
| Site x Date | 3 | 0.19 | 5.14 | 0.0163 | 0.60 | 1.8 | 0.0435 |
| Error: Day x Reps/Site | 12 | 0.15 | | | 0.60 | 7.2 | |
| Depth | 2 | 1.16 | 34.13 | 0.0001 | 0.76 | 1.5 | 0.0006 |
| Site x Depth | 2 | 0.13 | 3.85 | 0.0675 | 0.76 | 1.5 | 0.0887 |
| Error: Depth x Reps/Site | 8 | 0.14 | | | 0.76 | 6.1 | |
| Date x Depth | 6 | 0.06 | 1.05 | 0.4213 | 0.34 | 2.1 | 0.3959 |
| Site x Date x Depth | 6 | 0.09 | 1.52 | 0.2132 | 0.34 | 2.1 | 0.2743 |
| Error: Date x Depth x Reps/Site | 24 | 0.24 | | | 0.34 | 8.2 | |

Table A2.2. Single degree of freedom contrasts for significant sources of variation in water-filled porosity.

| Source | d f | SS | F | Pr>F |
|---|---|---|---|---|
| Date | 3 | 0.48 | 12.69 | 0.0000 |
| Linear | 1 | 0.05 | 4.40 | 0.0579 |
| Quadratic | 1 | 0.42 | 33.31 | 0.0001 |
| 3rd order | 1 | 0.01 | 0.38 | 0.5510 |
| Error: Day x Reps/Site | 12 | 0.15 | | |
| Site x Date | 3 | 0.19 | 5.14 | 0.0163 |
| Site x Linear | 1 | 0.01 | 0.23 | 0.6368 |
| Site x Quadratic | 1 | 0.15 | 12.38 | 0.0042 |
| Site x 3rd order | 1 | 0.03 | 2.79 | 0.1207 |
| Error: Day x Reps/Site | 12 | 0.15 | | |
| Depth | 2 | 1.16 | 34.13 | 0.0001 |
| Linear | 1 | 1.15 | 67.55 | 0.0000 |
| Quadratic | 1 | 0.01 | 0.72 | 0.4214 |
| Error: Depth x Reps/Site | 8 | 0.14 | | |

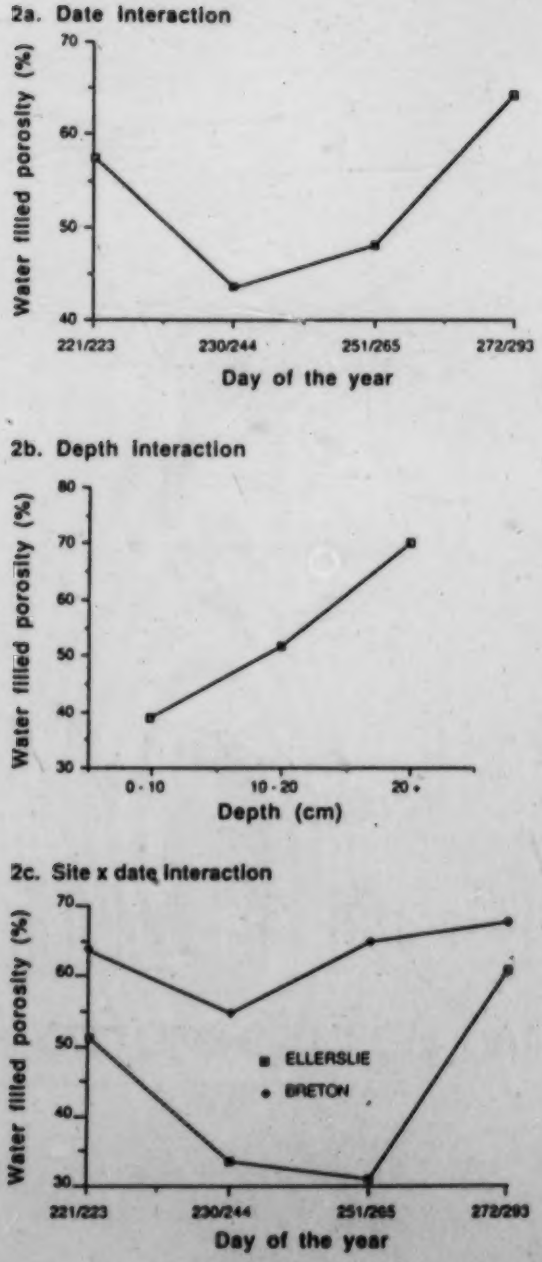


**Figure A2.1. Date, site by date, and depth interactions for water filled porosity at Ellerslie and Breton.**